



ATLAS OF THE LEAF ANATOMY IN PENTASCHISTIS

R.P. Ellis and H.P. Linder

MEMOIRS OF THE BOTANICAL SURVEY OF SOUTH AFRICA No. 60
MEMOIRS VAN DIE BOTANIESE OPNAME VAN SUID-AFRIKA No. 60

ATLAS OF THE LEAF ANATOMY

IN

PENTASCHISTIS

(ARUNDINEAE: POACEAE)

by

R.P. ELLIS* and H.P. LINDER**

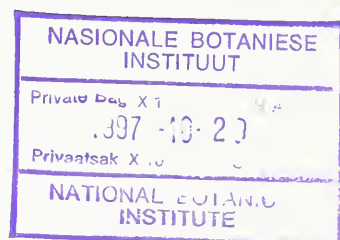
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Abstract

ELLIS, R.P. & LINDER, H.P., 1992. Atlas of the leaf anatomy in *Pentaschistis* (Arundineae: Poaceae). *Memoirs of the Botanical Survey of South Africa* No. 60, pp. 314.

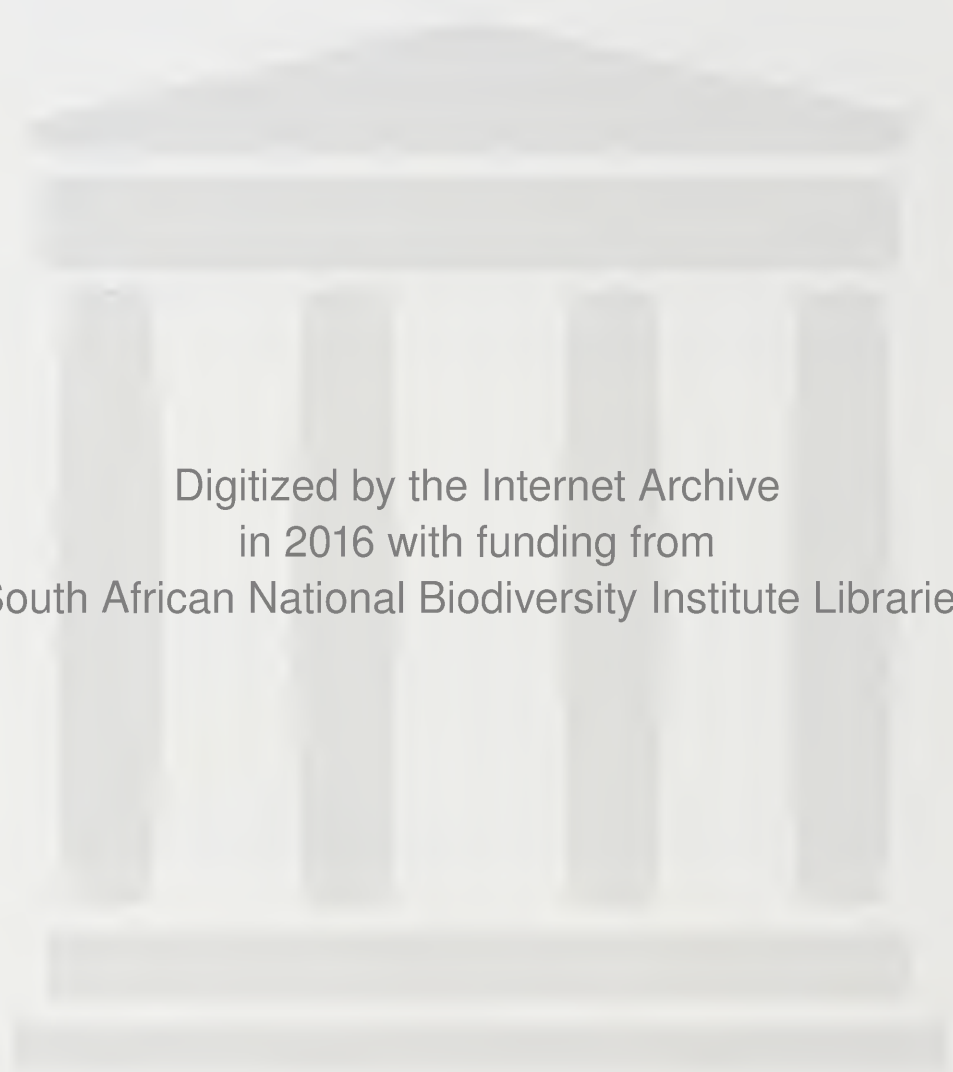
In a recent revision of the genus *Pentaschistis* (Linder & Ellis 1990a), leaf blade anatomy was used extensively as evidence for the delimitation of the 68 species recognised. The present work visually presents these anatomical data in support of the taxonomic decisions taken in the revision. A total of 220 plates is included, incorporating 1 243 photomicrographs, illustrating the leaf blade anatomy in transection, the abaxial epidermis under the light microscope as well as both epidermides as seen under the scanning electron microscope. A total of 622 voucher specimens, all collected in the field, were examined by these methods. This sample included 64 of the 68 species of *Pentaschistis*.

The results show very close congruence between leaf anatomy and morphology at the species level. However, the species groups based on morphological criteria are not strongly supported by the anatomical evidence. A brief classification of the taxa based on this evidence is presented for comparison with the informal morphological groupings. The leaf anatomy also suggests close affinities for some *Pentaschistis* taxa with neighbouring arundinoid genera such as *Prionanthium*, *Merxmuellera* and *Pentameris*. This study indicates that generic realignments are needed in the southern African Arundineae to reflect phylogenetic lineages.

Uittreksel

In 'n onlangse hersiening van die genus *Pentaschistis* (Linder & Ellis 1990a), is die anatomie van die blaarskyf op groot skaal gebruik vir die afbakening van die 68 spesies wat erken word. Die onderhawige werk bied hierdie anatomiese data visueel aan ter ondersteuning van die taksonomiese besluite wat in die hersiening geneem is. Altesaam 220 plate, saamgestel uit 1 243 mikroskoopfoto's, illustreer die blaarskyfanatomie in dwarssnede, die abaksiale epidermis onder die ligmikroskoop asook albei epidermisse soos hulle onder die aftaselektronmikroskoop vertoon. 'n Totaal van 622 verwysingseksemplare, wat almal in die veld versamel is, is deur middel van hierdie metodes ondersoek. Hierdie materiaal het 64 van die 68 *Pentaschistis*-spesies ingesluit.

Die resultate toon 'n noue ooreenstemming tussen blaaranatomie en morfologie op die spesievlak. Die spesiegroepe gebaseer op morfologiese kenmerke, word egter nie sterk deur die anatomiese gegewens ondersteun nie. 'n Beknopte klassifikasie van die taksons gebaseer op hierdie gegewens, word gegee vir vergelyking met die informele morfologiese groeperings. Die blaaranatomie dui ook op noue verwantskappe van sommige *Pentaschistis*-taksons met naasliggende arundinoïede genusse soos *Prionanthium*, *Merxmuellera* en *Pentameris*. Hierdie ondersoek toon dat hergroeperings in die Arundineae van Suider-Afrika benodig word om hul filogenetiese herkoms te weerspieël.



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Introduction

The publication of a detailed atlas of the leaf blade anatomy of the genus *Pentaschistis* is considered essential for the following reasons:

(i) the correct delimitation of the species of this large genus has generally proved to be difficult when based on morphological criteria only (Chippindall 1955; Clayton & Renvoize 1986). However, in a recent revision of *Pentaschistis* (Linder & Ellis 1990a), leaf anatomy was used extensively in the circumscription of species. Anatomical information proved invaluable in defining specific taxon limits and this anatomical evidence needs to be published to support and justify many of the taxonomic decisions taken. The species groups within *Pentaschistis*, proposed by Linder & Ellis (1990a), are also based extensively on as yet unpublished anatomical evidence.

(ii) the correct circumscription of the genus *Pentaschistis* poses difficulties. Clayton & Renvoize (1986) consider *Pentaschistis* to be a homogeneous genus yet it is not clearly separable from closely related arundinoid genera. This problem extends beyond *Pentaschistis* to the generic groupings within the Arundinoideae which are not adequately supported by empirical data (Kellogg & Campbell 1986) and there has been no taxonomic stability in the *Danthonia*–*Rytidosperma*–*Merxmuellera* complex. The apparent stability in the delimitation of *Pentaschistis* is misleading and stems from a lack of critical study and information. This detailed presentation of leaf anatomy in *Pentaschistis* should provide an objective basis for integration of anatomical data into any phylogenetic analysis of the genus or the tribe Arundineae.

(iii) detailed studies of the leaf anatomy of most of the other southern African arundinoid genera have already been published: *Dregeochloa* (Ellis 1977), *Merxmuellera* (Ellis 1980a, b; 1981a, b; 1982a, b; 1983), *Centropodia* (Ellis 1984, 1989a), *Pseudopentameris* (Ellis 1985a), *Pentameris* (Ellis 1985b–d, 1986a), *Elytrophorus* (Ellis 1986b), *Urochlaena* (Ellis 1988a), *Chaetobromus* (Ellis 1988b) and *Prionanthium* (Ellis 1989b). Comparable information on *Pentaschistis* is required for integration with the results of these previous studies.

Although *Pentaschistis* is a relatively large genus with 68 species, very little has been published on its leaf anatomy, and Metcalfe (1960) refers to only a single paper. In this work De Wet (1956) studied 38 species and noted that all had festucoid mesophyll (=non-Kranz anatomy)

and most had elongated microhairs with a tapering distal cell and dumbbell-shaped silica bodies i.e. a panicoid epidermis. On this basis the genus was regarded as belonging to the Danthoneae of the Arundinoideae rather than the Aveneae of the Pooideae. However, in eight species, arundinoid links were not so evident, as microhairs were not found and the silica bodies were spherical.

A detailed study of the leaf anatomy of 36 species of *Pentaschistis* was undertaken by Robbertse (1959) but regrettably, this is unpublished. The observations of this study are largely in agreement with those of the present study and it is unfortunate that these results have had to wait 30 years before being confirmed and published. Such unique characters as multicellular glands, linear glands and the elongated microhairs with minute apical cells are illustrated in this work but their taxonomic significance has not been appreciated by subsequent workers. The observations of Robbertse (1959) will be referred to wherever relevant, as the names of the voucher specimens have all been updated and his findings can thus be readily integrated with the present ones.

(iv) anatomical character variability within taxa is often not sufficiently appreciated by agrostologists (Davila & Clark 1990) and there is a definite need for more extensive sampling of plants within a species and of species within a genus or subgenus in studies of micromorphology.

In the past there has been a tendency to use single specimens as being representative of species or even genera. However, the treatment of the observed variation will be entirely dependent on knowledge of how a particular character varies within a taxon (Kellogg & Campbell 1986). Thus, if a genus is described as variable for a character, it may mean that single plants exhibit both character states, or that some plants within a species have one character state while others have another, or that some species have wholly one state and others another state. Leaf anatomy in *Pentaschistis* very clearly illustrates all three possibilities, even with the same characters at different taxonomic levels such as the genus, species groups (sections), and species. The publication of a detailed atlas of leaf blade anatomy of as many species of *Pentaschistis* as possible, including inter- and intraspecific variation where relevant, is essential for an understanding of anatomical character state evolution in the genus. This is particularly relevant if done in conjunction with a phylogeny of the species within the genus, as is the aim of this project. It is essential to determine the primitive

state of all characters in the genus in order for them to be used in later phylogenetic analyses. Such conclusions are only possible if sufficiently representative anatomical samples are studied as is the case with many of the *Pentaschistis* species illustrated in this study.

(v) ecological anatomical adaptations can often be very confusing in comparative anatomical studies. *Pentaschistis* illustrates examples of this phenomenon very clearly. Thus species with wide ecological tolerances ranging from the lower, drier, hotter rainshadow areas to higher, wetter, colder alpine habitats very often exhibit similar adaptations to both these extremes. These adaptations include many anatomical features such as: narrower, thicker inrolled or infolded leaf blades; adaxial ribs and furrows are more prominent; supporting tissue is better developed with sclerenchyma girders being larger; the mesophyll tissue tends to be more compact and the costal zones are generally wider than the intercostal zones. Epidermal cell walls and cuticles are thickened and this is generally associated with sinuous anticlinal walls. This structural convergence in leaf anatomy between grasses from different habitats very often makes interpretation of the anatomy difficult. In these instances it is essential that detailed provenance information be consulted before systematic deductions can be made. This type of similar anatomical response to differing environmental variables is probably widespread but is often overlooked in taxonomic studies incorporating anatomical information.

(vi) the photographic evidence presented enables the reader to make his own observations and to draw his own conclusions. This visual presentation of data also makes long detailed descriptions superfluous.

Materials and methods

Descriptive data of leaf blade anatomy for all the *Pentaschistis* taxa studied is stored in the DELTA system (Watson & Dallwitz 1988) together with morphological and available cytological information. The anatomical character list is given in Table 1, using the standardized terminology and character state definitions of Ellis (1976, 1979). All this information, in combination, will be used in an effort to arrive at more natural generic delimitations of *Pentaschistis* and allied genera. Detailed anatomical descriptions on computer diskette are available from the authors and will not be repeated here.

TABLE 1.—*Pentaschistis* delta anatomical character list

LEAF IN TRANSVERSE SECTION

1. (anatomical type)/
 1. mesic leaf type/
 2. intermediate leaf type/
 3. sclerophyllous leaf type/
2. leaf outline (width)/
 1. expanded/ dep. 2,1:4
 2. setaceous/ dep. 2,2:3
3. (expanded, open blade)/
 1. flat/
 2. V-shaped/
 3. U-shaped/
 4. inrolled margins/
4. (setaceous, filiform, infolded blade)/
 1. V-shaped (lamina folded)/
 2. U-shaped (lamina rolled)/
 3. terete/
5. margin/
 1. thickened/
 2. abrupt and not tapering/
 3. gently tapering/
 4. a pointed projection/
6. adaxial ribs and furrows (presence)/
 1. absent (surface not ribbed)/ dep. 6,1:7
 2. slight/
 3. medium/
 4. massive with cleft-like furrows/
7. adaxial furrows (distribution)/
 1. located between all vbs/
 2. located over 3'vbs/
 3. present on either side of midrib only/
8. abaxial surface (ribs and furrows - presence)/
 1. not ribbed/
 2. with ribs and furrows/
9. (median vascular bundle)/
 1. median vb only present (same as 1'vbs)/
 2. midrib present (no associated parenchyma)/
 3. keel present (colourless parenchyma associated with midrib)/
10. (number of 1'vbs in leaf section)/
 - 1'vbs in leaf section/
11. (number of smaller bundles between 1'vbs)/
 - 3'vbs between successive 1'vbs/
12. (position of vbs in leaf blade)/
 1. all vbs situated in centre of blade/
 2. all vbs closer to abaxial surface/
 3. all vbs closer to adaxial surface/
 4. vbs of different orders at different levels/
13. 1'vbs (description)/
 1. circular in outline/
 2. elliptical in outline/
14. (phloem)/
 1. sclerosed phloem present/
 2. no intrusive fibres in phloem/
15. metaxylem vessels/
 1. narrow (narrower than obs cells)/
 2. of medium diameter (width equal to obs cells)/
 3. wide (width greater than obs cell diameter)/
16. (extent of) outer bundle sheath/
 1. entire/
 2. with adaxial interruption only/
 3. with abaxial interruption only/
 4. with adaxial and abaxial interruptions/
17. bundle sheath extensions/
 1. absent/
 2. present (describe)/
18. outer bundle sheath cells/
 1. inconspicuous (resemble chlorenchyma cells/
 2. conspicuous (larger than chlorenchyma cells and lack chloroplasts)/
19. (sclerenchyma girders and strands)/
 1. all vbs with girders and strands/
 2. only 1'vbs with girders and strands/
20. adaxial sclerenchyma as/
 1. small strands/
 2. small girders/
 3. girders narrowing towards vbs/
 4. T-shaped or inversely anchor-shaped girders/

21. abaxial sclerenchyma as/
 1. small strands/
 2. narrow girders/
 3. shallow girders/
 4. trapezoidal girders/
 5. linked girders, forming continuous subepidermal layer/
 6. continuous subepidermal layer not linked to vbs/
22. chlorenchyma of/
 1. diffuse parenchyma cells with intercellular air spaces/
 2. large angular parenchyma cells with intercellular air spaces/
 3. small, angular isodiametric cells with small air spaces/
23. abaxial epidermal cells (size)/
 1. all larger than adaxial ones/
 2. of intercostal zones only larger than adaxial ones/
 3. similar in size to adaxial epidermal cells/
24. abaxial epidermis with (epidermal appendages)/
 1. no epidermal appendages/
 2. cuticular papillae/
 3. prickles/
 4. multicellular glands/
 5. cushion based macrohairs/
 6. superficial macrohairs/
25. adaxial epidermis with (epidermal appendages)/
 1. no epidermal appendages/
 2. inflated papillae/
 3. prickles/
 4. multicellular glands/
 5. cushion based macrohairs/
 6. superficial macrohairs/
60. Girders of/
 1. collenchyma/
 2. sclerenchyma fibres/
61. Secondary walls of girder cells/
 1. lignified/
 2. of cellulose/
62. Massive ribs/ dep. 6,4:62
 1. flat-topped/
 2. rounded/

ABAXIAL EPIDERMIS IN SURFACE VIEW

26. epidermal zonation/
 1. differentiated/
 2. not differentiated/
27. intercostal long cells (shape)/
 1. rectangular (parallel side walls)/
 2. hexagonal (side walls angled)/
 3. inflated (side walls bowed)/
28. intercostal long cell (length)/
 1. elongated (length greater than 3x width)/
 2. slightly elongated (length less than 3x width)/
 3. cubical (length = width)/
 4. short, vertically elongated (length less than width)/
29. intercostal long cell (wall thickness)/
 1. walls unthickened/
 2. walls slightly thickened/
 3. walls moderately thickened/
 4. walls heavily thickened/
 5. walls pitted/
30. intercostal long cells (wall undulations)/
 1. straight/
 2. slightly undulating/
 3. moderately sinuous/
 4. deeply sinuous/
31. (associated cells in long cell files)/
 1. long cells adjoin one another/
 2. single short cells between successive long cells/
 3. pairs of short cells between successive long cells/
 4. cork-silica cell pairs between successive long cells/
 5. single silica bodies between successive long cells/
 6. hooks between successive long cells/
32. stomata/
 1. absent/
 2. low dome-shaped/
 3. high dome-shaped/
 4. tending to parallel sided type/
33. stomatal files/ dep. 32,1:33
 1. separated by more than one file of long cells/
 2. separated by one file of intercostal long cells/
 3. adjoin one another/
34. papillae/
 1. absent/
 2. thickened cuticular, many per cell/
35. prickles (ignore margin)/
 1. absent/
 2. costal, with short barbs/
 3. intercostal, small, with long barbs/
36. microhairs (description)/ dep. 36,1:37
 1. bicellular/
 2. absent/
37. (microhairs description continued)/
 1. with basal and distal cell of equal length/
 2. with basal cell slightly longer than distal cell/
 3. with basal cell much longer than distal cell/
 4. with basal cell shorter than distal cell/
38. macrohairs (description)/ dep. 38,3:39-40
 1. stiff with thick walls/
 2. soft with thin walls/
 3. absent/
39. macrohairs (description continued)/
 1. base bulbous/
 2. base constricted/
 3. base undifferentiated/
40. macrohairs (description continued)/
 1. associated with a raised cushion/
 2. associated with a few raised epidermal cells/
 3. not associated with specialized epidermal cells/
41. multicellular glands (description)/ dep. 41,1:42
 1. absent/
 2. stalked with bulbous head/
 3. crateriform, unstalked/
 4. sunken below the level of the epidermis/
 5. sessile and linear/
42. multicellular glands (location)/
 1. occurring on margins only/
 2. occurring above vbs only/
 3. marginal and associated with the vbs/
43. silica bodies (description)/(costal only)/
 1. absent/
 2. tall and narrow/
 3. round, single/
 4. round, enfolded by cork cell/
 5. kidney shaped/
 6. irregularly dumbbell-shaped/
 7. angular dumbbell-shaped/
 8. elongated dumbbell-shaped/
 9. elongated, nodular/

ULTRASTRUCTURE (SEM)

ABAXIAL SURFACE

44. Stomata/
 1. absent/
 2. flush with epidermis/
 3. overarched by inflated papillae/
45. Papillae/
 1. absent/
 2. small, cuticular/
 3. inflated/
46. Prickle hairs/
 1. absent/
 2. with short barbs/
 3. with long barbs, macrohair-like/
47. Microhairs/
 1. absent/
 2. with distal and basal cell equal in length/
 3. with distal cell longer than basal cell/
 4. with distal cell shorter than basal cell/
 5. with very short distal cell, elongate/
48. Macrohairs/
 1. absent/
 2. stiff with distinct raised cushion/
 3. flexible with few specialized epidermal cells associated with base/
49. Multicellular glands (description)/ dep. 49.1:50
 1. absent/
 2. stalked with bulbous head/
 3. unstalked, crateriform/
 4. sunken/
50. Multicellular glands (location)/
 1. occurring on margins only/
 2. occurring on margins and above vbs/
51. Epicuticular wax/
 1. absent/
 2. present as fine, thin platelets/
 3. present as thick, dense rods/

ADAXIAL SURFACE

52. Stomata/
 1. absent/
 2. flush with epidermis/
 3. overarched by inflated papillae/
53. Papillae/
 1. absent/
 2. small, cuticular/
 3. inflated/
54. Prickle hairs/
 1. absent/
 2. with short barbs/
 3. with long barbs, macrohair-like/
55. Microhairs/
 1. absent/
 2. with distal and basal cell equal in length/
 3. with distal cell longer than basal cell/
 4. with distal cell shorter than basal cell/
 5. with very short distal cell, elongate/
56. Macrohairs/
 1. absent/
 2. stiff with distinct raised cushion/
 3. flexible with few specialized epidermal cells associated with base/
57. Multicellular glands (description)/ dep. 57.1:58
 1. absent/
 2. stalked with bulbous head/
 3. unstalked, crateriform/
 4. sunken/

58. Multicellular glands (location)/
 1. occurring on margins only/
 2. occurring on margins and above vbs/
59. Epicuticular wax/
 1. absent/
 2. present as fine, thin platelets/
 3. present as thick, dense rods/

In this paper only brief written discussions on outstanding anatomical attributes, variation in character states, differences and similarities in relation to other taxa and interspecific variation are included. Detailed photomicrographs comprehensively illustrate the anatomy of all the taxa studied and **the captions elaborate on the anatomical structure**. This atlas also visually demonstrates some of the intraspecific variation observed in some species. By presenting the data visually it is hoped to show that anatomical characters are subject to the same constraints and limitations as any others—an enormous degree of anatomical variability exists in *Pentaschistis* and is undoubtedly of taxonomic significance. Many species are linked by similar distinct anatomical characters and this may indicate relationships. Generally the congruence between the anatomical indications and those from morphology is close and these two character sets usually corroborate one another. Where the character sets are not congruent, further studies are suggested to develop a more natural classification of the genus.

Field collection of fresh leaf blade material was done largely on a geographical basis, covering the distribution range of each species as fully as possible. Generally 1–3 plants were sampled per population and, therefore, this data cannot be used to analyse intra-populational variation although insight was sometimes gained at this level. The emphasis was on comparison between species, and the field collections were conducted accordingly. The voucher specimen provenances are cited following the quarter-degree square reference system of Edwards & Leistner (1971).

Specimens of *Pentaschistis* species were collected in the field throughout South Africa during the period 1971 to 1989. A total of 622 specimens was collected, representing all southern African taxa of the genus. Herbarium voucher specimens were prepared as verification for the names used for these specimens and all are cited in Linder & Ellis (1990a). They are housed in the National Herbarium (PRE).

Leaf blade segments, approximately 20 mm long, were removed from the central part of basal culm leaves and immediately fixed in FAA (Johansen 1940). Transverse sections, 10 µm thick, were prepared after desilicification in 30% hydrofluoric acid (Breakwell 1914), dehydration using the method of Feder & O'Brien (1968) and infiltration and embedding in Tissue Prep (Fisher Scientific). The sections were stained in safranin and fast green (Johansen 1940). The manual scraping method of Metcalfe (1960) was used to prepare scrapes of the abaxial epidermis. These were either double-stained in methylene blue and ruthenium red or only in safranin. The anatomical structure was recorded photographically using a Reichardt Univar microscope and Ilford Pan F film (ASA 50).

The material fixed in FAA was also used for ultrastructural studies with a scanning electron microscope. The leaf blade segments were dehydrated in 2,2-dimethoxypropane (Merck) for two hours and then placed in 100% acetone for five minutes following the method of Neumann *et al.* (1982). The material was critical point dried with liquid CO₂ at 85 atmospheres at 40° C after which it was mounted on aluminium stubs with double-sided tape. Preparations were either stored in a dessicator with silica gel or observed directly with an ISI SX-25 scanning electron microscope operated at 25 kV accelerating voltage. Cuticular structure was photographed with a 6 × 7 cm camera

on Ilford FP4 120 film at varying magnification.

The taxa are numbered in the same way as in the revision of the genus by Linder & Ellis (1990a). The figures which appear at the back of the book are numbered correspondingly, and the page numbers appear beneath the species heading in the text. All figures of *Pentascistis pallida*, for example, are numbered 7 with a–g referring to the seven informal forms recognized within this species. Where several figures are used to illustrate a taxon these are numbered sequentially, for example 7b.1–5. In this way the anatomical observations can be easily integrated with the revision of the genus.

Mesic and sclerophyllous leaf blade anatomy

Two basic types of leaf blade anatomy can be recognised in the South African arundinoid grass genera—the mesic (or orthophyllous) and the sclerophyllous type (Ellis 1988a; Linder & Ellis 1990b). In most arundinoid genera only one or the other of these types is encountered, but both types occur in *Pentaschistis*. It is therefore necessary to define and describe them, as their differing cellular organization and tissue distribution patterns will be implied whenever these terms are used. *Ehrharta*, of the Bambusoideae, is also heterogeneous for these two types (Gibbs Russell & Ellis 1987).

The two types differ not only in their anatomy but also in morphology and ecology (Table 2) and they appear to belong to two distinct evolutionary lineages evident in the South African Arundineae. *Pentaschistis* is the only genus in this tribe with representatives in both categories, and careful evaluation of the mesic and sclerophyllous taxa will undoubtedly be informative in arriving at a more natural circumscription of the genus and allied arundinoid genera.

Morphologically the mesic leaf type is typically soft, thin and expanded, although it may become infolded or inrolled under adverse moisture conditions. It is short-lived and persists for only a single growing season or part thereof. The sclerophyllous leaf, on the other hand, is tough, coriaceous, thick and permanently infolded, being acicular, filiform or setaceous. This leaf type is probably long-lived, persisting for more than one growing season.

Anatomically the mesic leaf type has uniformly distributed, diffuse mesophyll tissue with no regular pattern of arrangement of the relatively large parenchyma-like chlorenchyma cells. This tissue occupies most of the space between the usually widely spaced vascular bundles. An extensive intercellular air space system is also present. The sclerophyllous type contrasts with this in having a very compact mesophyll of small isodiametric cells with minute intercellular air spaces. Much of the tissue between the closely spaced vascular bundles may also be sclerenchyma girders and, together with the very deep adaxial furrows, this results in the mesophyll being confined to a few cell layers adjacent to the vascular bundles and below the furrows.

The widely spaced vascular bundles of the mesic type are usually associated with small sclerenchyma girders or even small strands. Adaxial ribbing is typically not prominent and bulliform cells are in wide fans of small to medium-sized cells. In sclerophyllous leaves the vascular bundles are always associated with conspicuous

sclerenchyma girders, these often fusing to form a continuous abaxial hypodermal layer. This abundant sclerenchyma tissue may be either lignified or have cellulose secondary cell walls. The adaxial surface is usually deeply grooved with groups of small bulliform cells at the bases of the furrows. The difference in the degree of development of the sclerenchyma tissue is one of the most conspicuous differences between these two types.

Another major difference between these two types is the epidermal structure. In the mesic type the cuticle is thin

TABLE 2.—The major differences between the mesic and sclerophyllous leaf types in the South African Arundineae

Mesic type	Sclerophyllous type
Pentaschistis	Pentaschistis
<i>Tribolium</i> <i>Chaetobromus</i> <i>Karoochloa</i> <i>Schismus</i> <i>Urochlaena</i> <i>Prionanthium</i>	<i>Merxmuellera</i> <i>Pentameris</i> <i>Pseudopentameris</i>
Short-lived leaves—persist for single season or part thereof	Long-lived leaves—persist for more than one growing season
Soft, thin leaf blades—usually expanded and open	Tough, coriaceous, thick leaves—usually setaceous, filiform or acicular
Diffuse mesophyll of large rounded parenchyma cells	Compact mesophyll of small isodiametric cells
Extensive intercellular air space system	Minute intercellular air spaces
Sclerenchyma only associated with the bundles as girders or strands	Sclerenchyma abundant—often continuous between bundles
Cuticle and outer walls of epidermal cells thin	Cuticle plus outer epidermal cell wall thickened
Abaxial stomata present	Abaxial stomata absent
Epidermal zonation evident	No distinction between costal and intercostal zones in surface view
Common in lowland fynbos and succulent karoo	Common in mountain fynbos
Clay and shale soils	TMS derived sands

and the epidermal cells have unthickened walls, whereas in the sclerophyllous type the cuticle is well developed and/or the epidermal cells have thickened outer walls. In addition, stomata are usually present on the abaxial epidermal surface in the mesic leaf type, whereas they are generally absent in the sclerophyllous types. There are exceptions in this regard, however.

Epidermal zonation is clearly evident in the typical mesic type with wide intercostal zones and narrow costal zones which are only 3–5 cell files wide. The intercostal long cells are unthickened with only slightly sinuous anticlinal walls. Abaxial microhairs are usually present. In the sclerophyllous type, epidermal zonation is often not evident due to the underlying hypodermal layer. When present, the intercostal zones are generally narrower than the wider costal zones. The long cells themselves have thickened, deeply sinuous walls which may even be pitted. Abaxial microhairs are rare.

Various levels of intermediacy often occur between the mesic and sclerophyllous types, particularly in *Pentaschistis*. However, the diffuse and compact nature of the chlorenchyma appears to be a consistent feature separating these two types. Sclerophyllous species generally have thick outer epidermal cell walls plus cuticles, compact mesophyll, abundant sclerenchyma and thicker leaves. However, these characteristics occur in different combinations in different species but they all serve to impart the typical hard, coriaceous texture associated with the leaves of sclerophylls in general.

Ecologically the mesic type is associated with clay and shale soils of lowland fynbos and succulent karoo which

have a higher nutrient status than the oligotrophic soils with which taxa with the sclerophyllous leaf type are associated. These taxa usually occur on sands derived from Table Mountain Sandstone in the mountain fynbos which are deficient in nitrogen and phosphate. The unique vegetation of the Cape Floristic Region is characterized by sclerophyllous leaves, and the anatomy of this type in the associated grasses appears to be an analogous development and may reflect an equivalent response by these grass taxa to these particular environmental conditions. Sclerophylly in these conditions is not necessarily an adaptation to drought, as is generally believed, but possibly represents an adaptation to nutrient poor environments (Medina *et al.* 1990) and probably serves to 'safeguard' scarce nutrient resources.

The anatomy of the mesic type is associated with genera such as: *Tribolium* Desv., *Chaetobromus* Nees, *Schismus* Beauv., *Karoochloa* Conert & Turpe, *Urochlaena* Nees, *Prionanthium* Desv. as well as many species of *Pentaschistis*, including all the taxa of Group 1. The sclerophyllous type, on the other hand, is found in *Merxmüllera* Conert, *Pentameris* Beauv., *Pseudopentameris* Conert and most species of *Pentaschistis* included in Groups 3–6.

The terms mesic and sclerophyllous types therefore imply fundamental differences in leaf blade anatomy as well as leaf morphology and ecology and, in the genus *Pentaschistis* in particular, may prove to be systematically very important. These two terms imply fundamental structural differences and their use makes it superfluous to describe various attributes which, in combination, constitute these two basic leaf types. A clear understanding of these two types is essential to fully appreciate the differences between the anatomical groupings in *Pentaschistis*.

Anatomy of the species of *Pentaschistis*

Group 1

This group includes all those species with stalked multicellular glands. This gland type exhibits a variety of forms (Linder *et al.* 1990) and all these variations occur in this species group. The raised glands are common on leaf blades and are visible in leaf blade transections, abaxial epidermal scrapes and particularly under the SEM. A modification of this stalked gland type, the sunken crypt-like gland (Linder *et al.* 1990), is also included in this group. Species with sessile, linear glands as well as the eglandular species are excluded from this species group and are placed in Groups 2–6. A few species lacking foliar glands, but possessing inflorescence glands, are included in this group.

All taxa included in this group also have the mesic or orthophyllous type of leaf anatomy which is fully described and discussed in the introduction. Most Group 1 taxa have typical mesic leaf anatomy (Ellis 1988a; Linder & Ellis 1990b) but various levels of intermediacy often occur between this mesic type and the alternative sclerophyllous type. However, the nature of the chlorenchyma cells (diffuse or compact) is the most reliable means of distinguishing between these two basic leaf types, and all Group 1 taxa have diffuse mesophyll.

Although mesic-type leaf blades may be narrow and setaceous due to inrolling, they are not of the permanently infolded, acicular type which is common in species with sclerophyllous anatomy. Two Group 1 exceptions to this are *Pentaschistis cirrhulosa* and *P. lima* which have setaceous leaves as well as stalked crateriform glands (Linder & Ellis 1990a). In these taxa, although the leaf outline resembles the sclerophyllous type, the diffuse nature of the mesophyll tissue reveals that this is indeed of the mesic type.

The mesic leaf type in *Pentaschistis* is also largely correlated with the dumbbell type of silica body. This is in contrast to the sclerophyllous species groups (Groups 3–6) where dumbbell-shaped silica bodies are very rare.

These dumbbell-shaped silica bodies are often very variable, even along a given cell file. The dumbbells may be tall with short constrictions or longitudinally elongated without noticeably constricted central portions. On a given leaf, cross-shaped, angular and even nodular types may occur as well as variable dumbbell types. The dumbbell

silica bodies in *Pentaschistis* never have the classical 'dog bone' shape of the typical panicoid dumbbell silica body. Silica body shape is not diagnostically useful for defining the taxa of this group except where modifications of the basic mesic type occur. In these cases silica body shape is often also modified and may even be of the tall and narrow paired type.

In contrast to species Groups 2–6, where individual species are often recognizable due to distinct diagnostic anatomical features, the species of Group 1 all share very similar anatomy and usually cannot be assigned to subgroups, or distinguished to species level on anatomical criteria alone. They usually differ only in the degree of expression of the anatomical character set. Although many trends are evident, these are not exclusive to any given subgroup or species. A significant proportion of the specimens of any taxon invariably exhibit some intermediate character states.

The variation in the anatomical characters of the taxa of Group 1 often appears to be clinal, being correlated with the geographical or ecological distribution of the species. Sometimes the variation occurs within populations, however, and then may be a result of inherent variability in the species. Before the leaf blade anatomy of the taxa of this species group can be appreciated, intensive sampling is needed even within populations. It is not possible to appreciate this type of variability using under-represented anatomical samples and single specimens cannot be considered to be representative of a species unless this is shown by adequate sampling. A satisfactory classification of this group will necessitate detailed biosystematic studies which is beyond the scope of this work.

This variability is in marked contrast to Groups 2–6 where, very often, a single specimen is sufficient to understand the anatomy of a species and additional replicates contribute very little additional information. In Group 1, on the other hand, even with fairly large samples it is still not possible to determine whether the observed variation is due to geographical, ecological, seasonal, age or positional factors.

Group 1A

This group includes the taller, more robust species (more than 200 mm tall) with leaves 3–6 mm wide. The spikelets

are relatively large, being more than 5.5 mm long. The specific limits of many of the species are difficult to define (Linder & Ellis 1990a) and many specimens cannot be confidently assigned to species. Similar patterns are exhibited by the leaf anatomy which is typically that of Group 1, both in its mesic structure and possession of glands, as well as in its variation patterns.

Only stalked glands occur in this group, sunken glands being absent. These glands are common, generally occurring on the leaf blade margin where the glands may be stalked or the stalks may be reduced, resulting in the sessile, wrap-around type. All intermediate developmental stages occur and glands are even absent on the leaf blades in some species or specimens.

Group 1A could be considered as one extreme of a morphological cline in which the largest plants with the largest spikelets are grouped. Group 1B is then intermediate for plant size, leaf width and spikelet size and Group 1C is the other extreme with small plants with small spikelets. This variation pattern might be correlated with longevity—from long-lived perennials to short-lived perennials to annuals—which in turn may be linked with climate or ecology. Size and longevity are not necessarily correlated but, generally, the larger, perennial Group 1A species occur in the moister habitats and the annual Group 1C species in drier or more fertile localities. This type of moisture and fertility gradient exists from the moist, mesic southern Cape northwards to the drier Namaqualand and Karoo regions and Groups 1A, 1B and 1C broadly follow this pattern.

The anatomical evidence does not fully support the three species groups as differentiated on morphological criteria (Linder & Ellis 1990a) as several character states are shared between a few species of each of Groups 1A, 1B and 1C, rather than occurring exclusively within any one of these species groups. A number of characters thus cut across the subgroups rather than being consistent within them. The type of macrohair and the presence and distribution of different types of glands are examples of characters which are not congruent with those morphological characters diagnostic for the subgroups of Group 1. This appears to indicate that several closely related taxa occur independently along the whole moisture gradient and are artificially separated into these species groups. This implies that there is a corresponding decrease in plant and plant part size with a decrease in moisture (or possibly plant age). It is therefore possible, that species with significantly different growth forms, plant and spikelet sizes, actually belong together rather than with species which share similar morphological characters such as spikelet size. This will make key construction and species group diagnoses very difficult and a final decision must await a synthesis of the anatomical data and all other relevant information.

1 *P. veneta* Linder

pp. 82–87 (Linder & Ellis 1990a: 29)

This species typically has classical mesic-type leaf anatomy. It is described and illustrated by Robbertse (1959)

as *P. rupestris*. His observations on marginal glands, sclerenchyma distribution, diffuse mesophyll, irregular dumbbell silica bodies and finger-like microhairs compare very well with the findings of the present study.

A trend is evident within *P. veneta* from the typical mesic leaf type to narrower, more rigid leaves in which the sclerenchyma supporting tissue is more extensive, the cuticle thicker, ribs and furrows more prominent and the costal zones much wider. The intercostal long cell walls are also much more sinuous. This trend is illustrated in transection in Figure 1.1A–J and the abaxial epidermis in Figure 1.2A–H.

In many grass taxa this type of structural trend, with an increase in xerophytic features, is associated either with increasing aridity or with altitude. However, in *P. veneta* the two extremes (Figures 1.1A, B & I, J and 1.2A, B & G, H) originate from the same population and morphologically, these two plants are very similar although the specimen with typical mesic anatomy does have softer, more flaccid leaves. It appears, therefore, that there is no ecological or geographical basis for this variation and as such, it is not considered to be significant taxonomically.

Marginal leaf glands are very common in *P. veneta* and they are present on all the specimens examined. Abaxially situated glands are not present but a single specimen with a narrow sclerified leaf (Figure 1.1J), has unusual adaxial glands located on the ribs situated laterally in the leaf.

This adaxial location of glands is very rare in the genus, and has only been recorded in a few specimens of each of the following taxa: the northern strandveld form of *P. barbata* subsp. *barbata* (Figures 2a.7A, B; 2a.8D, F), *P. pallida* form F (Figures 7f.1G, H; 7f.2E, F) and some specimens of *P. tomentella* (Figure 10.2A–D). This distinctive gland type, apart from its location on the leaf, is not clavate but dome-shaped and no surface cell detail is visible with the SEM (Figures 2a.8F; 10.4I).

All the plants with this type of gland come from the northern parts of the winter rainfall area from both the coastal lowlands and the mountains of the northern Cederberg and Namaqualand. They do not occur on white soils derived from TMS sandstone but on humic black sands in the Cederberg and granitic soils in Namaqualand and the coastal lowlands.

This distinctive gland type is consequently, not diagnostic for any particular taxon but only occurs on atypical specimens of each of four taxa from Groups 1A and B. However, specimens with this gland type are all from the same general geographic area and may be adapted to higher soil nutrition levels.

It should also be noted that the morphological limits between all these species are difficult to define, and the possibility of misidentifications must be considered. *P. barbata* subsp. *barbata*, *P. pallida* form F, *P. tomentella* and *P. veneta* all seem to intergrade in the Clanwilliam–Van Rhynsdorp–Nieuwoudtville area. The possibility of segregating these intermediates into a separate fifth taxon

was considered but did not appear to be a practical solution and was found to result in even more difficulty with species delimitation and separation.

The macrohairs of *P. veneta* may also indicate affinities. The long, stiff macrohair, with thickened walls and a constricted base (clearly illustrated in Figure 1.2B) inserted into a cushion of raised epidermal cells, does not occur widely in the genus. Other species which share this hair type are: *P. patula* form C (Figure 12c.2), *P. pallida* form B (Figure 7b.5), *P. pallida* form G (Figure 7g.2) and *P. densifolia* (Figure 8.2D). These hairs are common in all these taxa and they also occur in *P. barbata* subsp. *barbata*, but only in the montane form (Figure 2a.1D & H), and rarely in *P. rupestris* (Figure 5.2B). This macrohair type does not occur elsewhere in the genus although very similar hairs (in which the base is inflated and not constricted) may be confused with this hair type.

This macrohair type, therefore, links a small, ephemeral annual with a small, short-lived perennial with a larger perennial from Groups IC, B and A. These taxa may form part of a continuum and may be artificially separated morphologically. They also all possess marginal glands with long stalks and occur in the west and north-west of the fynbos biome. A grouping of these taxa in the same species group is indicated by this anatomical evidence and groups 1A, B and C may be artificial as presently defined.

P. veneta, therefore, shows strong links with *P. pallida* form B and *P. patula*. However, *P. veneta* also interfaces with *P. pallida* form F, and others, on the basis of adaxial dome-shaped glands. Thus the anatomical evidence of these two characters (adaxial glands and macrohairs) is contradictory and needs to be fully integrated with all other evidence before final relationships become clear.

A close relationship between *P. veneta* and the montane form of *P. barbata* subsp. *barbata* is also indicated by both morphology and anatomy. Their anatomy is identical except that glands were not observed on the leaf segments of the small sample of the montane form of *P. barbata* studied, but both possess cushion-based macrohairs. In fact the montane form of *P. barbata* would fit more readily into *P. veneta* on the basis of leaf anatomy than it does with any of the other forms of *P. barbata*, all of which exhibit varying degrees of sclerification and do not have macrohairs. These other forms of *P. barbata* also all occur in lowland communities (particularly the Coastal Fynbos and Strandveld) and not in mountain fynbos as do both *P. veneta* and the montane form of *P. barbata*. More information on these taxa is required before final decisions can be taken.

SPECIMENS EXAMINED

CAPE.—3219 (Wuppertal): Cederberg, Duiwelsgat between Sneeuweb and Uitkyk Pass, (—AC), Ellis 5594, 5595, 5596. 3318 (Cape Town): Stellenbosch, (—DD), Adamson 4075. 3319 (Worcester): Groot Winterhoek Wilderness Area, valley between Drosterberg and Groenberg, (—AA), Ellis 5490, 5497; Franschoek, Adolfskop, (—CC), Linder 4601; Worcester, Keeromsberg, (—DA), Linder 4414.

2a *P. barbata* (Nees) Linder subsp. *barbata* pp. 88–94 (Linder & Ellis 1990a: 31)

This taxon is difficult to delimit and exhibits an enormous range of variation. Populations from the West Coast strandveld and sandveld fall into a variable group which differs considerably from populations from the foothills of the surrounding mountains. This morphological variation pattern is mirrored in the leaf anatomy.

Four anatomical forms (Table 2a), each associated with a different habitat type can be recognized:

(i) Montane form: soft, flaccid, expanded mesic leaves; cushion-based macrohairs common (Figure 2a.1); from low altitude mesic mountain fynbos on the foothills of the mountains, generally on soils derived from granite.

The distribution overlaps with that of *P. veneta* and the leaf anatomy in the area of sympatry is very similar, except that this montane form was not observed to have glands. They both have very similar cushion-based macrohairs and their leaf cross-sections are very similar. This resemblance is fully discussed under *P. veneta*.

(ii) Sandveld form: expanded but rigid leaves which tend to fold under moisture stress (Figures 2a.2; 2a.3); no glands were observed on the anatomical preparations although distinct yellow imprints were left on the drying paper during pressing and the plants have a characteristic odour; the illustrations of Robbertse (1959) under *P. angulata* appear to apply to this form; from coastal fynbos of the sandveld of the West Coast; in fine, loose tertiary sands.

This form constitutes the central core of this species and does not resemble any other *Pentstemon* species very closely. The anatomy is intermediate between that of the other three forms and is rather variable with abaxial stomata being present or absent and with the prickles being very variable in size and location. The leaf transections are very uniform however, with medium ribs and furrows and with typical diffuse mesophyll.

(iii) Strandveld form: expanded, tough eglandular leaves which inroll tightly under conditions of moisture stress (Figure 2a.4A); a psammophyte from the coastal strandveld on unstabilized sea dunes.

The anatomy is unusual for the mesic type in that a continuous subepidermal sclerenchyma layer is usually developed, with a consequent absence of abaxial stomata and epidermal zonation (Figure 2a.5). The blades are also often tightly inrolled with a thick cuticle—resembling the sclerophyllous type. The mesophyll, nevertheless, remains diffuse and not compact as in the sclerophyllous leaf type. This anatomy appears to be an adaptation to high salinity. This form is very close to the sandveld form and these two intergrade in most respects.

(iv) Northern strandveld form: expanded glandular leaves (Figure 2a.7); from the strandveld in the St Helena Bay area on soils derived from granite. This form does not differ morphologically from the sandveld form.

The anatomy resembles that of the sandveld form most closely but the massive ribs and deep furrows and the sclerenchyma girders are better developed. Foliar glands

were observed on this form. These dome-shaped adaxial glands, in particular, suggest links to *P. veneta* from the Cederberg (Figure 1.IJ), *P. pallida* form F 'pillansii' also from the Cederberg (Figure 7f.IG, H) and *P. tomentella* from Namaqualand granitic soils (Figure 10.2A–D). This type of adaxial gland is restricted to a few specimens of each of these few species. This unusual gland type is, therefore, not diagnostic for any particular taxon but all the specimens with these glands come from the same general geographical area. The taxonomic significance, if any, of these glands is uncertain at present.

P. barbata subsp. *barbata* is therefore, a very difficult entity to define anatomically, especially as the excessive variation has such a strong ecological and geographical basis. The indications from the leaf anatomy are that each of these forms could also be recognised as subspecies. However, if this is done then cognisance must also be taken of the close anatomical resemblance between the montane form of *P. barbata* and *P. veneta*, as these two taxa may be more naturally placed together outside *P. barbata*.

SPECIMENS EXAMINED

CAPE.—3218 (Clanwilliam): St Helena Bay, (–CC), *Ellis 5132+*, 5801+. 3318 (Cape Town): 10 km W of Hopefield, (–AA), *Ellis 5134, 5135*; 7 km E of Hopefield, (–AB), *Ellis 5136*; Yzerfontein, (–AC), *Ellis 1684***; Rondebeg, between Atlantis and Yzerfontein, (–AD), *Ellis 5802*; Table Mtn, above Kirstenbosch, (–CD), *Ellis 2305**; Bloubergstrand, *Ellis 2359***, 2360**, 5803**, 5804**; Jonkershoek, (–DD), *Ellis 2219**, 2234*.

* mesic, soft montane form.

** eglandular, strandveld form.

+ northern strandveld form with adaxial glands.

2b *P. barbata* (Nees) Linder subsp. *orientalis* Linder

pp. 95, 96 (Linder & Ellis 1990a: 31)

This subspecies is only known from vegetated coastal sand dunes in the Goukamma Nature Reserve near Knysna. It is very poorly known and fresh material was only collected for this study at the type locality where a small population still survives.

The leaf anatomy is typical of that of the mesic type, the wide, expanded leaves having very diffuse mesophyll tissue, alternating first and third order vascular bundles (Figure 2b.1) but the abaxial epidermis is very unusual in having few or no stomata (Figure 2b.2). However, epidermal zonation into costal and intercostal zones is evident, which is often not the case in species without abaxial stomata. Abaxial microhairs were also not observed. Marginal leaf glands do occur, these are only slightly raised on short stalks (Figures 2b.1A; 2b.2C).

The habitat of subsp. *orientalis* is very similar to that of the strandveld form of *P. barbata* subsp. *barbata* as they both inhabit coastal sea dunes. However, subsp. *barbata* has strongly inrolled leaves with considerable abaxial sclerenchyma development such that epidermal zonation is usually not evident (Figures 2a.4; 2a.5). This structure strongly resembles the sclerophyllous anatomical type, whereas subsp. *orientalis* has most of the attributes of the mesic type of leaf anatomy. Both subspecies possess very

few abaxial stomata however. These significant differences in leaf anatomy are possibly correlated with rainfall differences between the South Coast Knysna Forest and the much drier succulent strandveld of the West Coast. The separation of these two taxa is, therefore, fully supported by the anatomical evidence.

Subsp. *orientalis* resembles the montane form of subsp. *barbata* more closely in leaf anatomy except that it does not have cushion-based macrohairs or numerous abaxial stomata. Subsp. *orientalis* also possesses foliar glands which were not observed on the montane form of subsp. *barbata*. This also suggests that subsp. *orientalis* is distinct from the montane form.

The recognition of subsp. *orientalis* as a geographical subspecies is certainly supported by the anatomical evidence but the indications are that these two taxa should be treated as distinct species. However, subsp. *orientalis* is so poorly known due to its rarity and restricted distribution, that this suggestion is based on material from only a single population. Additional material is required before more definite decisions can be made. Greater clarity on the affinities of subsp. *orientalis* will undoubtedly help in understanding species delimitations and relationships in the very variable *P. barbata*.

SPECIMENS EXAMINED

CAPE.—3422 (Mossel Bay): Goukamma Nature Reserve, (–BB), *Ellis 6002*, Linder 5049.

3 *P. aspera* (Thunb.) Stapf

pp. 97–99 (Linder & Ellis 1990a: 32)

P. aspera has distinctive mesic-type anatomy, modified somewhat from the typical condition. The blade is relatively thick with uniform well-developed rounded adaxial ribs and narrow furrows associated with all vascular bundles across the entire leaf width (Figure 3.1A, C). The margin is noticeably abrupt and does not taper at all (Figure 3.1B, D, E). This ribbed, thicker leaf is the usual type for this species and occurs on plants growing in post-fire fynbos, while occasionally, from shady places, the leaves can be thinner, with shallower ribs and wider furrows (Figure 3.1C, D).

The nature of the marginal glands is diagnostic for this species. This saddle type of gland, which is wrapped around the margin and in which the subglandular cells are very short, is only found on *P. aspera* (Figures 3.1B, D, E; 3.2C; 3.3F). This gland type is clearly illustrated in Robbertse (1959). As the subglandular cells are not elongated, no stalk is developed. This is even the case when these glands are not located on the leaf margin but are situated costally below the vascular bundles on the abaxial surface (Figures 3.1F; 3.2A, B). These abaxial glands are only slightly raised and typically have a flat surface and are neither concave or convex. The gland cells comprise a single flat layer and are surrounded by a ring of collar cells (Figure 3.2A–C). This unusual gland type if further discussed in Linder *et al.* (1990).

This gland type is restricted to *P. aspera* but *P. longipes* has glands tending to this type. A notable exception is a single specimen of *P. pallida* form B (Figures 7b.4A, C; 7b.5A). In this specimen the abaxial glands in particular, are identical to those of *P. aspera*. Morphologically this *P. pallida* specimen cannot be accommodated in *P. aspera* as the growth form is quite distinct and the shared possession of this unique gland type apparently has no taxonomic significance.

These glands are common in *P. aspera* and were observed on all the specimens studied anatomically, particularly the marginal glands which result in a pseudo-serrate margin being visible. Very few other species of *Pentastichis* have such a high occurrence of glands, whereby they are visible on all serial sections and epidermal scrapes which include the margin.

The microhairs of *P. aspera* are of interest due to their unusually large size, being up to four times longer than the stomatal subsidiaries. This longer type of microhair tends to be associated with the larger plants of Group 1A, *P. aspera* in particular, as well as *P. papillosa*, *P. rupestris* and *P. longipes*. However, the microhairs of *P. veneta* and *P. barbata* are much smaller. Microhairs in Groups 1B and 1C are generally somewhat smaller although some specimens of *P. pallida* form B (Figure 7b.2D) and *P. pallida* form F (Figure 7f.3F) have equally large microhairs. Microhair size, therefore, is another character which tends to vary continuously from Group 1A through Groups 1B and 1C. The relative lengths of the basal and distal cell of the microhairs of *P. aspera* are more or less equal, as in *P. rupestris* and *P. barbata*, whereas the distal cells are much smaller in *P. papillosa*. In *Pentastichis* the microhair size and type is remarkably variable, even on a single leaf, and this conflicts with the generally held belief that microhairs are characters of fundamental systematic importance in the Poaceae (Johnston & Watson 1976), but they appear to be taxonomically unimportant in *Pentastichis*.

P. aspera is morphologically similar to *P. papillosa* but can be easily distinguished by leaf anatomy—the shape of the adaxial ribs and furrows is clearly different, the type of microhair differs, and the occurrence of marginal glands varies between these two species. Marginal glands always occur on *P. aspera*, whereas they are very rare in *P. papillosa*, and when present, are not of the saddle type.

Thus, although these two species are similar morphologically, a very close relationship is not supported by the leaf anatomy. Anatomical evidence suggests very close affinities between *P. longipes* and *P. aspera* as both have abrupt margins with saddle-glands, similar ribs and furrows, abaxial stomata are common and the microhairs are very similar. A comparison of Figures 3.1–3.3 with 6.1–6.3 clearly illustrates this anatomical congruence.

SPECIMENS EXAMINED

CAPE.—3318 (Cape Town): Table Mtn, Platteklip Gorge, (—CD), *Ellis* 5575, below Saddle, *Linder* 4337. 3418 (Simonstown): Cape Peninsula, Scarborough, (—AB), *Ellis* 5437; Cape Point lighthouse, (—AD), *Ellis* 2323, 2328, *Taylor* 8033; False Bay, Cape Hangklip, behind sea dunes, (—BD), *Ellis* 2337, Betty's Bay, Harold Porter Garden, *Ellis* 5540. 3419 (Caledon): Kleinmond, behind sea dunes, (—AC), *Ellis* 679.

4 *P. papillosa* (Steud.) Linder pp. 100–103 (Linder & Ellis 1990a: 32)

P. papillosa can easily be distinguished anatomically from *P. aspera* (which it resembles morphologically) by the large, flat-topped adaxial ribs, cleft-like furrows, tapering margins and the virtual absence of glands. These features are also described in Robbertse (1959) under *P. subulifolia*. Distribution and habitat of these two species are almost identical, extending from the Cape Peninsula eastwards along the coastal shelf as far as Hermanus where they are found on lower slopes in TMS derived soils. Although this degree of geographical and ecological overlap is unusual in *Pentastichis*, there is strong anatomical evidence that these two species are not particularly closely related. This may help explain their apparent interspecific habitat competition.

The markedly ribbed leaf outline of *P. papillosa* is reminiscent of the transectional anatomy of several other species—*P. pallida* form C 'albescens' (Figure 7c.1) and *P. heptamera* (Figure 67.1) in particular. *P. oreodoxa* (Figures 23.1; 23.2), *P. setifolia* (Figure 24.1) and *P. glandulosa* (Figure 26.1) also resemble this type of anatomy; however, in these latter species, glands are often present (either stalked clavate or sunken crateriform), the ribs are rounded and there is a tendency in all for the development of a continuous hypodermal sclerenchyma layer with a corresponding loss of abaxial epidermal zonation and stomata. This latter trend was not observed in *P. papillosa* where the large abaxial trapezoidal girders do not fuse laterally and stomatal files occur on all epidermides.

Interestingly, the adaxial T-shaped girders virtually adjoin one another on either side of the cleft-like furrows (Figure 4.1D), thus the adaxial surface effectively has a continuous sclerenchyma layer, particularly under conditions of water stress. The reason for this parallel development on opposite leaf surfaces is not apparent, especially as all these leaves show inrolling in response to moisture stress. In *P. papillosa* this inrolling is such that the opposite margins meet, forming a hollow, canaliculate leaf (Figure 4.1C).

The microhairs of *P. papillosa* deserve comment. They are unusually large and long as in *P. aspera*, being up to 4 × longer than the stomatal complexes (Figure 4.2F), but differ structurally from those of other Group 1A species in that the distal cell is noticeably shorter than the basal cell (Figure 4.3B, C, F, G) as shown in Robbertse (1959) as well. In the other Group 1A taxa the basal and distal cells are of equal length. This difference in the proportions of the two microhair cells may be phylogenetically meaningful as microhair structure and type is considered to be taxonomically significant (Amarasinghe & Watson 1988). Amongst the glandular *Pentastichis* species, *P. galpinii*, *P. natalensis*, *P. oreodoxa*, *P. setifolia*, *P. ampla* and *P. glandulosa* have similar microhairs. In addition these taxa resemble *P. papillosa* in overall anatomy.

P. papillosa, therefore, appears to be a good species and the anatomical indications are that it is not particularly

closely related to *P. aspera*. From this study it is not apparent to which species it is phylogenetically linked but the indications are that these should be sought with some of the summer rainfall glandular species belonging to Groups 1F and particularly 1D & E. Affinities with the taxa of Group 1A do not appear to be particularly close. It, nevertheless, has diffuse mesophyll tissue of the mesic type, although the rest of the anatomy shows xerophytic trends such as increased sclerenchyma development and deep, narrow adaxial furrows. This, together with the rare occurrence of multicellular marginal glands, unambiguously confirms its placement in Group 1 but its more precise affinities remain unclear.

SPECIMENS EXAMINED

CAPE.—3418 (Simonstown): Cape Peninsula, Simonstown, Red Hill, (—AB), *Ellis* 2311, Scarborough, *Ellis* 5436, 5439, Silvermine, *Ellis* 547, 5442; False Bay, Cape Hangklip, (—BD), *Ellis* 2516, 3419 (Caledon); Ratelrivier, (—CA), *Ellis* 5989.

5 *P. rupestris* (Nees) Stapf

pp. 104–112 (Linder & Ellis 1990a: 34)

This species has distinctive mesic-type leaf anatomy but differs slightly from the typical anatomy of Group 1A in having well-developed supporting tissue, very diffuse mesophyll tissue (very often with the chlorenchyma cells appearing to be collapsed) and a rather thick abaxial cuticle. This latter attribute appears to be linked to the thickened, sinuous anticlinal walls of the intercostal long cells which typify this species. Glands and macrohairs, although sometimes present, are generally absent.

Although the anatomy of this species is recognizable and distinguishes it from the other species of Group 1A, individual specimens exhibit considerable variation. This variation, however, does not appear to be taxonomically important although it may be visually impressive. Thus anatomical differences between specimens with open, expanded leaves (Figures 5.1–5.3) and those with inrolled leaf blades (Figures 5.4–5.6), although of a magnitude equal to or greater than between some other species of *Pentaschistis*, appear to reflect only habitat differences as this type of variation changes continuously with altitude and substrate. The great visual impact of these apparently taxonomically insignificant anatomical differences clearly demonstrates the need to study a sufficiently representative sample of any species before the anatomy can be adequately appreciated. This is essential for merely compiling anatomical descriptions and may not be adequate for understanding the variation and its taxonomic implications.

From this anatomical study it appears as if *P. rupestris* is a good, if variable, species. This species occurs from the Cederberg southwards as far as Touwsrivier, but it is very rare south of the Cederberg. The anatomical sample comes mainly from Cederberg localities but specimens from the Groot Winterhoek Mountains and the Bokkeveld were studied.

Within the Cederberg *P. rupestris* is very common, occupying a variety of habitats and gives the impression

of being in the process of expanding its ecological range. This may be indicative of recent ecological disturbance in this area and, given the wide phenotypic plasticity exhibited by *P. rupestris*, this species appears capable of increasing its ecological tolerance in the Cederberg.

Although specimens with rolled leaves occur mainly away from the Cederberg and can be recognized morphologically, there are specimens with identical anatomical outlines which originate in the Cederberg as shown in Figure 5.4 where E and F are from the Cederberg and A–D come from the Bokkeveld and the Porterville areas. The inrolled leaf condition, therefore, appears to occur throughout the distribution range of *P. rupestris* but open, expanded leaves may be limited to mesic sites in the Cederberg.

Macrohairs, although very rare in *P. rupestris*, may indicate affinities with other taxa of Group 1A, *P. veneta* in particular. As discussed under the latter species, a group of species from Groups 1A, B and C share very similar macro-hairs which do not occur elsewhere in the genus.

The multicellular microhairs (Figures 5.2H; 5.3C) sometimes present on specimens of *P. rupestris* are very unusual. As far as is known, no other grass apart from *Guadua* (Soderstrom & Ellis 1986) has such microhairs. These hairs can consist of more than three cells. The *Guadua*leae is a primitive bambusoide tribe which cannot be placed in the core Bambusoideae partly because of its unique microhairs. Some other *Pentaschistis* species with this odd microhair type were rarely observed. Examples are: *P. pallida* form F 'pillansii' (Figure 7f.5D), *P. pallida* form G 'silvatica' (Figure 7g.2F) and *P. airoides* (Figure 13a.3B).

SPECIMENS EXAMINED

CAPE.—3219 (Wuppertal): Cederberg, Algeria, Cederberg Pass, (—AC), *Ellis* 2505, 2507, 5504, Welbedacht, *Ellis* 5506, Helshoogte Pass, *Ellis* 5587, 5788, 5792, Sneeuberg Hut, Duiwelsgat, *Ellis* 5593, 5597*, 5598*; Groot Winterhoek Mts, Suurvlek Farm, (—CC), *Ellis* 5484*; Kouebokkeveld, Elim Farm, (—CD), *Ellis* 5577*.

* specimens with inrolled, xeric leaves.

6 *P. longipes* Stapf

pp. 113–115 (Linder & Ellis 1990a: 35)

This species, although rather distinct morphologically, is very rare and poorly known. Fortunately a single population was located in 1989 at Brakduine near Oyster Bay in the Humansdorp District from which material for anatomical study was obtained. This represents only the third known collection of this species. It occurs on vegetated coastal dunes where it is found in grassland between bush clumps.

Anatomically *P. longipes* resembles *P. aspera* rather closely. Both species have the mesic anatomical type, the leaf blade is relatively thick, ribs and furrows are well developed but the furrows are not cleft-like, the leaf margins do not taper, marginal glands without subglandular tissue (Figure 6.1B) are common and the microhairs are large. The abaxial epidermis has many stomata

and the long cells are moderately sinuous with the undulations having shallow amplitudes, short wave-lengths but with a high frequency. The marginal glands of *P. longipes* differ from those of *P. aspera* in not being of the wrap-around type but tend to be located abaxially at the margin (Figure 6.1B). They, nevertheless, are not raised on stalks, and appear to be a slight modification of the *P. aspera* type of stalked gland.

The abaxial microhairs of *P. longipes* are large with the basal cell noticeably shorter than the distal cell (Figure 6.3B). This type differs substantially from the microhairs of *P. papillosa* where the distal cell is relatively short in comparison with the basal cell. The adaxial microhairs of *P. longipes* are much narrower, but longer, than those on the abaxial surface (Figure 6.3D).

P. longipes seems to be correctly placed in Group 1A and its affinities probably lie with *P. aspera*. However, additional populations must be located before a better appreciation of its affinities can be gained.

SPECIMENS EXAMINED

CAPE.—3424 (Humansdorp): Brakduine to west of Slang River, Oyster Bay, (—BB), Ellis 6006, Linder 5048.

Group 1B

This grouping includes those species with stalked glands but with plants smaller than those of Group 1A (Linder & Ellis 1990a). They are generally less than 200 mm tall with leaves less than 3 mm wide and with spikelets less than 6 mm long.

The leaf anatomy indicates that this is an artificial grouping, convenient for identification but not indicative of relationships. The species included in this group often exhibit anatomical similarities with species in either Groups 1A or 1C or even Group 3 in the case of *P. cirrhulosa* and *P. lima*.

Several of the species of this group are exceedingly variable in their morphology and this is also reflected in their leaf anatomy. This variation makes anatomical diagnoses impossible but, as the variation sometimes seems to be linked to distribution or ecology, it can be informative. Generally Group 1B can be considered as being intermediate to Groups 1A and 1C along several ecological or geographical gradients.

These interesting geographical patterns all occur away from the heartland of the fynbos biome viz: the area south of Porterville and extending as far east as Caledon. In this small area morphological and anatomical distinctions between the taxa of this group (as well as some taxa in groups 1A and 1C) are often not possible. However, to the east in the southern and eastern Cape, several rather distinct taxa occur but these intergrade westwards with plants from this core area. Likewise, along the more arid northern margin of the winter rainfall region, several taxa are distinguishable but these are linked to other taxa from the south. This results in indistinct boundaries between

many of the taxa of this group and consequently, the identification of specimens is very difficult, including the anatomical voucher specimens. The interpretation of the anatomical characters is arbitrary, as determination of the specimen name is likely to be based on variable and inconsistent characters. The species definition problems in these taxa need to be resolved using multivariate and biosystematic analyses, and a full range of morphological, anatomical and biological features, in order to determine the basic species boundaries. In the absence of this synthesis, the group has to be dealt with as being variable.

7 *P. pallida* (Thunb.) Linder

(Linder & Ellis 1990a: 36)

P. pallida is the core species of Group 1B. It is common throughout the winter rainfall area, usually at lower altitudes and particularly in physically disturbed sites. It is exceedingly variable and, consequently, very difficult to classify satisfactorily. It invariably comprises a major proportion of herbarium collections of *Pentaschistis* and likewise, of the anatomical vouchers used in this study. The recognition of seven informal forms* has enabled the 61 anatomical vouchers from this study to be discussed in manageable groups, which is undoubtedly more informative than lumping them all together in a variable species. Each form will be treated separately here for convenience and clarity.

The geographical patterns generally exhibited by Group 1B taxa are clearly evident in the leaf anatomy of *P. pallida*. Thus in the east and south, as well as along the more arid northern fringes of the fynbos, the seven forms are clearly recognisable but in the heartland of the fynbos biome their distinction and separation becomes arbitrary.

The relationships of *P. pallida* appear to be exceedingly complex and difficult to interpret, as each of the seven forms displays anatomical links to different *Pentaschistis* taxa. *P. pallida* is undoubtedly a species complex central to the entire Group 1 viz. species with stalked multicellular glands and with the mesic type of leaf anatomy. As such, a detailed understanding of the systematics of this important taxon is essential, but this will necessitate studies of variation at the population level, which are beyond the scope of this work. To illustrate the complexity of the inter-relationships of *P. pallida*, the anatomical indications will be briefly summarized to give perspective to the detailed discussions of each taxon which follow:

Form A 'brevifolia'—xeric anatomical modifications with very few leaf glands, from warmer, drier habitats. Intergrades with *P. pallida* form B.

Form B 'pallida'—several different anatomical trends are evident:

(a) xeric specimens with few or no glands from drier habitats. Resembles *P. pallida* form A, some specimens of *P. pallida* form F, *P. patula* form A 'patula' and *P. aristifolia*.

* named by codes A to G, but also given informal names cited in quotation marks.

(b) typical mesic specimens with glands and stiff macrohairs with constricted bases inserted into a raised cushion. Resembles some specimens of *P. veneta*, *P. rupestris* and *P. pallida* form F as well as *P. barbata* subsp. *barbata* (montane form), *P. densifolia* and *P. patula* form C 'heteroplo'. *P. pallida* form G 'silvatica' also has this macrohair type.

(c) mesic anatomy but with abaxial glands not raised on stalks and resembling those diagnostic of *P. aspera*. Very rare in *P. pallida*.

(d) xeric specimens from alpine habitats. Distinct anatomy not suggestive of links to any other Group 1 *Pentastichis* species. Possibly a distinct species linked to *P. montana* and possibly *P. lima* and *P. cirrhulosa*.

Form C 'albescens'—large ribs and furrows, tapering margins, abaxial hypodermal layer may be developed and leaf glands are absent. Distinct anatomy with fundamental differences to *P. pallida* form B. Anatomical resemblance to *P. papillosa* and *P. heptamera*.

Form D 'australis'—mesic anatomy but lacking abaxial stomata, nodular silica bodies and no leaf glands. Resembles *P. aurea* subsp. *aurea* and the other taxa of Group 2b which do not have stalked glands.

Form E 'angustifolia'—mesic anatomy with raised glands and macrohairs associated with a few inflated epidermal cells. Anatomy very similar to that of Group 1F taxa without sunken glands viz. *P. oreodoxa*, *P. setifolia* and *P. glandulosa*.

Form F 'pillansii'—anatomically intermediate between several groups of *Pentastichis* taxa:

(a) mesic to xeric anatomy with stiff macrohairs and raised glands. Tends toward *P. pallida* forms A and B and *P. densifolia*.

(b) soft macrohairs with swollen bases inserted between two inflated epidermal cells and fusiform long cells. Similar to *P. tomentella*.

(c) shared possession of the domed, adaxially located gland type. *P. veneta* (single specimen), *P. barbata* subsp. *barbata* northern strandveld specimens, some southern specimens of *P. tomentella* as well as *P. pallida* form F specimens from the Olifants River area.

(d) thick leaves with copious supporting tissue, sinuous thick-walled long cells and unusual three-celled microhairs are shared by some *P. pallida* form F specimens and *P. rupestris*.

Form G 'silvatica'—sessile, elongated leaf glands also occur on glumes of *P. natalensis*, *P. cirrhulosa* and *P. lima*. Epidermal pattern with fusiform long cells and absence of stomata similar to *P. pallida* form D. Stiff macrohairs with constricted bases similar to *P. pallida* form B.

The relationships of *P. pallida* are therefore, exceedingly complex and difficult to interpret. This study will merely describe the anatomical differences between the seven informal taxa and discuss structural similarities with other *Pentastichis* species, which will give a good indication of what other taxa must be included in any future taxonomic study of the *P. pallida* complex.

7a *P. pallida* form A 'brevifolia'

p. 116 (Linder & Ellis 1990a: 39)

P. pallida form A is very poorly represented in this study and only three specimens were assigned to this form. However, form A intergrades with form B, possibly along a grazing gradient, and several specimens placed in form B resemble form A very closely as a comparison of Figures 7a.1 with 7b.1 and 7b.2 clearly show.

Leaf blade glands are very rare or even absent in this form. Supporting tissue is well developed with prominent adaxial and abaxial girders and strands being present (Figure 7a.1B, D). Ribs and furrows are prominent, the margin is usually abrupt and the leaf blades are relatively thick. Costal zones are relatively wide (> 5 cell files) and the intercostal zones comprise five or less files of cells. The walls of the rather short long cells are thickened and sinuous (Figure 7a.1F), stomata are common and microhairs are infrequent. Macrohairs may be present (Figure 7a.1E, F) but generally are absent (Figure 7a.1G).

This anatomy indicates xerophytic adaptation in which the leaves are short and hard, all tissues are rather compact with thickened cell walls and the cuticle is thick. The Renosterveld habitat in the drier, hotter valleys, often in rain-shadow areas, is typical for this form which does not appear to occur on TMS derived soils but rather on shale bands or the richer valley soils. Both populations studied were from commercially grazed areas and this type of anatomy may be developed in response to grazing.

SPECIMENS EXAMINED

CAPE.—3218 (Clanwilliam): Piketberg, Versfeld's Pass, (—DD), Ellis 704. 3320 (Montagu): Barrydale, (—DC), Ellis 647. 3419 (Caledon): Gansbaai, (—CB), Ellis 5981.

7b *P. pallida* form B 'pallida'

pp. 117–125 (Linder & Ellis 1990: 40)

This form is a very variable entity which forms the core of *P. pallida*. Generally, it is a soft, caespitose, hairy form but a wide range of variation is included here and it intergrades with several of the other forms of *P. pallida*. It is widely distributed in the south-western Cape, from the Kamiesberg to the southern Cape forests and, consequently, occurs in a wide range of habitats at differing altitudes. It is very often associated with disturbance and is particularly common along roadsides in various soil types. This is typically a mountain fynbos species from the montane zone and often occurs on TMS soils. It appears to be replaced at higher alpine altitudes by other forms such as forms E and F.

Form B intergrades with form A 'brevifolia'. Figures 7b.1 and 7b.2 illustrate specimens which resemble form A in leaf anatomy (Figure 7a.1). None of these have leaf glands or macrohairs and they all exhibit various xerophytic attributes such as well-developed girders, ribs and furrows and shortened, thickened long cells with undulating walls. This anatomy is very similar to that of *P. patula* form A 'patula' (Figures 12a.1–3) and *P. aristifolia* (Figures 15.1; 15.2), two annuals from the arid north.

Five anatomical vouchers belong to this type and most of them resemble form A in morphology with short basal leaves but some have the cauline leaves typical of form B. From the provenances of the specimens it is also evident that these particular form B specimens often occur together with typical form A and/or typical form B plants. At the Piketberg locality, all three were found together, and the typical form B and this intermediate type occurred in close proximity at Jonkershoek. These observations strongly suggest that forms A and B cannot be satisfactorily separated and may merely represent the phenotypic expression of different grazing histories.

In this regard it is of interest to note the absence of glands in all these 'brevifolia'-like specimens. This may indicate that these structures have an antifeedant function, and that only *P. pallida* plants without glands are readily eaten.

The leaves of typical form B 'pallida' plants are generally wider and thinner than those which tend toward form A. This more mesic anatomy generally has less sclerenchyma, wider adaxial furrows and longer intercostal long cells with less sinuous anticlinal walls as shown in Robbertse (1959) under *P. thunbergii*. Associated with this mesic type anatomy are macrohairs (Figures 7b.3; 7b.5) and/or marginal, stalked glands (Figure 7b.4; 7b.5). These latter features are very rare in plants resembling form A in leaf anatomy but macrohairs were seen in typical form A plants (Figure 7a.1E, F).

Form B plants from higher altitudes also show xerophytic features which structurally resemble the form A type of anatomy. Examples are narrower and thicker leaves, abrupt margins and larger sclerenchyma girders with correspondingly wider costal zones. Examples are illustrated in Figures 7b.3F; 7b.4E & F and 7b.5C, D, G. All these leaves show similarities with the 'brevifolia'-type specimens except that they all also have glands or macrohairs or both.

The macrohairs of typical form B *P. pallida* are typically long and stiff with thickened walls and a constricted base inserted into a cushion of raised epidermal cells. This type of macrohair does not occur widely in the genus but is also found on *P. patula* (Figure 12.2) and *P. veneta* (Figure 1.2) as well as *P. densifolia* (Figure 8.2D). This hair type is also present on the leaves of *P. pallida* form G (Figure 7g.2C, D, E) but does not occur on any of the other *P. pallida* forms. The possible phylogenetic implications of the taxonomic distribution of this hair type are further discussed under *P. veneta*.

A single specimen, *Ellis* 2489, possesses some glands which are similar to those diagnostic for *P. aspera*. These glands without raised stalks are illustrated in Figures 7b.4A & C and 7b.5A. However, many of the marginal glands of this specimen are short-stalked and not of the wrap-around type characteristic of *P. aspera*.

The short, stiff cushion plants found at the upper altitudes of the Cape mountains which are included in form B appear to have a very distinct leaf anatomy as illustrated in Figure 7b.8. Unfortunately, only a single specimen of this type was available for study. Nevertheless the anatomy

of this specimen is very informative as to the degree of modification of the basic mesic type that is possible in response to harsh, alpine environments. The outline of the leaf of this specimen is essentially of the permanently infolded acicular type characteristic of the sclerophyllous anatomical type (Figure 7b.8A & B). A continuous abaxial hypodermal sclerenchyma layer is present with the corresponding absence of abaxial stomata (Figure 7b.8C & D). However, two attributes indicate the true nature of this unusual leaf: the mesophyll is not of the compact type and glands are present. This specimen appears to represent the extreme modification of the basic mesic leaf type. Additional collections of this taxon may justify its recognition as a separate species.

SPECIMENS EXAMINED

CAPE. —3218 (Clanwilliam): Piketberg, Versfeld's Pass, (—DC), *Ellis* 1176*, 5127. 3219 (Wuppertal): Cederberg, Pakhuis Pass, (—AA), *Ellis* 1162; Sneekop, (—AC), *Ellis* 5508; Citrusdal, Buffelsberg Pass, (—CA), *Ellis* 1191, 1192, Bokkeveld, *Ellis* 2489. 3318 (Cape Town): Table Mtn, Kirstenbosch, (—CD), *Ellis* 2306, 2307; Jonkershoek, Witbrug, (—DD), *Ellis* 2210*, 2215*, 2223, Jakkalsvlei, *Ellis* 2229, Heuningvlei, *Ellis* 2262*, 2263. 3319 (Worcester): 21km from Ceres on road to Worcester, (—CB), *Ellis* 1258; Keeromsberg, (—DA), *Linder* 4429+. 3323 (Willowmore): Uniondale, Uniondale Poort, (—CA), *Ellis* 5827*. 3418 (Simonstown): Simonstown, (—AB), *Ellis* 2312, 2316. 3419 (Caledon): Viljoen's Pass, (—AA), *Ellis* 5470.

* specimens resembling form A 'brevifolia'.

+ specimen with unusual sclerophyllous type anatomy.

7c *P. pallida* form C 'albescens'

pp. 126–128 (Linder & Ellis 1990a: 40)

This form is morphologically recognizable, being glabrous and eglandular with a compact, almost ovate inflorescence. It is restricted to the coastal lowlands from the Peninsula eastwards, where it occurs in limestone soils or coastal dunes. Typically the 'albescens' form is distinct from *P. pallida* form B, both morphologically and ecologically. It could be assigned to a separate species except that numerous intermediate specimens are known.

The leaf anatomy fully corroborates the above and the 'albescens' form is anatomically distinct from all the entities included in *P. pallida*. It has large, flat-topped adaxial ribs, cleft-like furrows, tapering margins and no leaf glands were observed (Figure 7c.1). Abaxially a hypodermal band of sclerenchyma may be developed (Figure 7c.1F) with a subsequent absence of abaxial stomata (Figure 7c.2A–D).

The leaf anatomy of this form is unusually uniform and consistently distinguishable with no sign of intermediate specimens in the sample of 16 specimens throughout the range of this form. This is in marked contrast to the morphology where there are so many intermediate forms that a clear delimitation is not possible.

It also seems unlikely that intermediate anatomical specimens of *P. pallida* form B will be found, as the basic leaf architecture of 'pallida' and 'albescens' differs considerably. Structures such as macrohairs and glands are not shared by both entities and the adaxial epidermides

differ greatly—compare Figure 7b.6D & E with Figure 7c.3D & E.

The two taxa also occupy completely different habitats with *P. pallida* 'pallida' being virtually restricted to mountain fynbos on TMS while 'albescens' occurs in coastal fynbos on calcareous substrates. This structural and ecological separation suggest that specimens with intermediate anatomy appear unlikely. This is supported by the findings of this study where the leaf anatomy of 'albescens' remained consistent throughout a fully representative sample.

The leaf anatomy of the 'albescens' form resembles that of *P. papillosa* most closely (Figures 4.1; 4.2). Whether this resemblance is indicative of close affinities between the two is unclear. *P. papillosa* does sometimes have leaf glands and soft macrohairs which do not appear to occur in 'albescens'. In addition, the microhairs of *P. papillosa*, with very short distal cells (Figure 4.3B, C, F, G), differ from those of *P. pallida* form C (Figure 7c.3C, F), where the basal cell is equal to, or shorter than, the distal cell. The two taxa are also ecologically separated and do not appear to be very closely related.

Plants of 'albescens' are sometimes confused with *P. heptamera*, a species which grows in similar habitat and resembles 'albescens' in vegetative morphology. The affinities of *P. heptamera* are uncertain and it has tentatively been placed in Group 6 due to its unique multiple-awned lemmas. However, the anatomical evidence strongly suggests that these two taxa are indeed closely related as a comparison of Figures 7c.1 and 7c.2 with 67.1 clearly shows. It is, however, possible that this anatomical similarity results from convergence to identical maritime arenicolous calcareous conditions inhabited by these two taxa. Further work is necessary to establish the phylogenetic relationships of *P. pallida* form C.

SPECIMENS EXAMINED

CAPE.—3418 (Simonstown): Cape Peninsula, Helderberg, (—AB), *Ellis* 2356, Cape Point, *Ellis* 2329; False Bay, Macassar Beach, (—BA), *Ellis* 5474, 5475, 5476; Cape Hangklip, (—BD), *Ellis* 2335. 3419 (Caledon): Gansbaai, (—CB), *Ellis* 5980. 3420 (Bredasdorp): De Hoop, Wydgelegen, (—AD), *Ellis* 1664, 5151, 5452, De Hoop Vlei, *Ellis* 2528; Skihaven turnoff, (—CB), *Ellis* 2535. 3422 (Mossel Bay): Sedgfield, (—BB), *Ellis* 5602, Goukamma, *Ellis* 6003. 3424 (Humansdorp): Cape St Francis, (—BB), *Ellis* 612; Oyster Bay, *Ellis* 6004.

7d *P. pallida* form D 'australis'

pp. 129–131 (Linder & Ellis 1990: 40)

This rather interesting taxon is recognised for the first time in this study. It appears to be relatively common in the southern Cape region and is found frequently in sunny localities in the Knysna forests, usually on roadsides or on shallow rocky soils without tall trees. The plants are glabrous without leaf glands and the awns are short.

Anatomically this taxon resembles the typical mesic type at first glance but closer examination reveals several unusual features, particularly of the abaxial epidermis: stomata are very rare and, when present, often deformed (Figure 7d.2B), the intercostal long cells are elongated and

distinctly fusiform in shape (Figure 7d.2A, C) and the silica bodies are often of the nodular type (Figure 7d.2C). The cuticle is also unusually thick for such a soft plant (Figure 7d.1B). No leaf glands were observed.

Surprisingly this anatomy resembles that of *P. aurea* subsp. *aurea* of Group 2b (with linear rather than stalked glands), and not that of any species in Group 1. The taxa of Group 2b also have very few abaxial stomata (and these are often deformed) and the intercostal long cells are fusiform in shape (Figure 40a.2). They also have a tapering margin (as is often the case in 'australis'), the same pattern of vascular bundle arrangement and a relatively thick cuticle. Both taxa have microhairs but no macrohairs. In all these respects *P. pallida* 'australis' matches *P. aurea* and some of the Group 2b taxa very closely and, anatomically these form a uniform group.

It appears as if raised multicellular glands do not occur on 'australis' and the awns are very reduced. In *P. aurea* the awns are absent and the 'australis' form may therefore, be considered to be an intermediate stage in the loss of the awns. This possibility warrants consideration and is consistent with the anatomical evidence.

Two other species also resemble *P. pallida* 'australis' somewhat in leaf anatomy viz. *P. pusilla* (Figure 49.1) and *P. capensis* (Figure 62.2). Both of these species are eglandular, belonging to Groups 3a and 5 respectively. However, the abaxial epidermis in particular is very similar to that of 'australis' as all have fusiform long cells, few or no stomata, microhairs and silica bodies which often are of the nodular type. These attributes in combination are very unusual but the leaf transverse sections show quite clearly that this resemblance is only superficial and unlikely to be taxonomically meaningful.

SPECIMENS EXAMINED

CAPE.—3322 (Oudtshoorn): George Dist., Montagu Pass, (—CD), *Ellis* 5823, 5825; Kaaimans River valley, (—DC), *Ellis* 5601, 5821. 3323 (Willowmore): Avontuur, (—CA), *Ellis* 5830.

7e *P. pallida* form E 'angustifolia'

pp. 132, 133 (Linder & Ellis 1990a: 40)

This taxon is very poorly represented in this study and it is not possible to draw firm conclusions from a sample consisting of only two specimens from the same locality. In addition this high altitude locality on the Swartberg is not typical of form E which is known from the southern Cape from Knysna to East London. The specimens studied anatomically, undoubtedly exhibit adaptations to a harsh alpine environment which will not be evident in specimens from lower altitudes.

Nevertheless a few observations can be made from the plants studied. The leaves are narrow and inrolled (Figure 7e.1A—D) with prominent girders associated with the first order vascular bundles. This structure can be explained in terms of the alpine habitat.

Morphologically the two specimens studied have typical setaceous leaves. The anatomy shows clearly that these

are not of the acicular, permanently infolded type but are involutely inrolled leaves of the mesic type. This xerophytic adaptation is probably in response to the extremes of the alpine environment and contrasts with that exhibited by species with the sclerophyllous type of anatomy in which the leaves are of the permanently infolded type (Ellis 1976).

The abaxial epidermis of 'angustifolia' (Figure 7e.1E–H) is very reminiscent of that of *P. oreodoxa* (Figure 23.3) and those specimens of *P. setifolia* (Figure 24.2) and *P. glandulosa* (Figure 26.3A–D) without the sunken type of gland. This includes all epidermal structures but the reduction in the length of the macrohairs is significant.

This observation corroborates the morphological indications as *P. pallida* 'angustifolia' is very difficult to tell apart from these latter three species. The collections studied may therefore, merely represent high altitude collections of either *P. oreodoxa* or *P. glandulosa* specimens without sunken glands.

Marginal short-stalked glands are present (Figure 7e.1 D, E) and these are very similar to those of *P. oreodoxa*. The transectional anatomy, with the tapering leaf margins, appears to be the only anatomical means of separating 'angustifolia' from these latter two species. However, a more representative anatomical sample is needed before this can be confirmed.

SPECIMENS EXAMINED

CAPE.—3321 (Ladismith): Swartberge, Swartberg Pass, (–BD), Ellis 5633, 5634.

7f *P. pallida* form F 'pillansii'

pp. 134–141 (Linder & Ellis 1990a: 41)

Morphologically this form is intermediate between *P. tomentella* and *P. rupestris* as well as *P. pallida* form B. This relationship is strongly supported by the anatomy which suggests, in addition, links to the northern strandveld form of *P. barbata* as well as *P. pallida* form A. *P. pallida* form F, therefore, approaches several other taxa of both Groups 1A and 1B and it links the northern Namaqualand Group 1 species with those from the south.

P. pallida 'pillansii' is found on the arid fringes along the western margins of the fynbos where it approaches both *P. tomentella* from Namaqualand and *P. barbata* from the Coastal Fynbos and the Strandveld. In the Cederberg links with *P. rupestris* are evident and, towards the southern margin of its distribution the populations resemble *P. pallida* form B. These trends are also strongly corroborated by the anatomy.

Similarities with *P. tomentella* include the rare domed adaxial glands (Figures 7f.1G, H; 7f.2E, F; 7f.4H; 10.2A–D; 10.4I, J) and the soft, flexible macrohairs with slightly swollen bases inserted between two inflated epidermal cells (Figures 7f.3D–H; 10.3A–H). Anatomical intergradation of these characters in these two taxa occurs in the region of sympatry between them viz. in the region of the Olifants River northwards to Nieuwoudtville. However, this is not exclusively so and 'pillansii' speci-

mens resembling *P. pallida* forms A and B are also found in this geographical area and do not possess this type of macrohair or the domed adaxial glands.

Anatomical resemblance to *P. rupestris* is evident in some specimens from the Cederberg as illustrated in Figure 7f.5. This anatomy is very similar to that of *P. rupestris* as illustrated in Figures 5.1–5.5. The thick, sinuous, rectangular walls of the long cells are very similar as are the stomata, silica bodies and large abaxial sclerenchyma girders. Of particular interest are the very unusual three-celled microhairs which are sometimes present (Figures 5.2H; 5.3C & 7f.5D). This microhair structure may just represent deformed hairs and, as such, should not be emphasized too much. Nevertheless, it is significant that they occur on these two taxa which also show overall anatomical resemblances. Three-celled microhairs are also rarely present on *P. pallida* form G 'silvatica' (Figure 7g.2F) and *P. airoides* (Figure 13a.3B).

P. pallida form F shares the rare domed adaxial glands with *P. tomentella* as well as the northern strandveld form of *P. barbata* (Figures 2a.7B; 2a.8D, E) and *P. veneta* from the Cederberg (Figure 1.1J). This very unusual gland location and type supports the suggested links between these taxa.

Yet other *P. pallida* form F specimens are close to *P. pallida* forms A and B in leaf anatomy as well as some specimens of *P. densifolia* (Figures 8.1G; 8.2B). Some of these specimens are without glands and macrohairs as is form A. Examples illustrated are Figures 7f.1A, B and 7f.3B which resemble form A closely (Figure 7a.1A–D, G). Others have macrohairs without glands as in Figure 7f.2A and 7f.3A, a condition sometimes present in both forms A and B (Figures 7a.1E, F; 7b.3; 7b.5C–H). No *P. pallida* form F specimens which resemble either of forms A and B have glands.

The stiff type of macrohair with a raised cushion base, which is characteristic of *P. pallida* form B (and also occurs on form A) is very rare in *P. pallida* 'pillansii' (Figure 7f.3A). Macrohairs in 'pillansii' are typically of the *P. tomentella* type in that they are soft and flexible with slightly swollen bases inserted between two inflated epidermal cells. These two distinct types of macrohair appear to be phylogenetically meaningful and the latter stiff, cushion-based type is discussed further under *P. pallida* form B.

P. pallida form F is therefore, a truly intermediate taxon intergrading morphologically and anatomically with several other taxa. In fact, the assignment of the form F specimens to the taxa which they resemble implies that no specimens will remain in this taxon. With all the specimens except those resembling *P. tomentella* this appears to be possible on the basis of morphology. However, the *P. tomentella*-like form F specimens do not have the fine grey covering of short hairs on the leaf blades and sheaths, a characteristic which is diagnostic for *P. tomentella*. Nevertheless anatomy reveals that hairs of identical structure, although much shorter than those of typical *P. tomentella*, do occur on those form F specimens which resemble *P. tomentella*. This suggests that these

specimens do actually belong to the same taxon and a broadening of the diagnosis of *P. tomentella* is required before they can be accommodated in this species.

Much more research is required before more meaningful decisions can be made regarding the correct taxonomic placement of the plants assigned to form F. The affinities of the taxa which appear to be linked together in this taxon at present are also not apparent. It is of interest to note that the anatomical results fully substantiate the morphological indications but it is not possible to find mutually exclusive morphological characters for separating these entities at present. Detailed studies of variation within populations and of ecological requirements are needed before reliable differences become evident. As presently constituted this taxon merely serves to emphasize the variability currently accommodated in *P. pallida*. Any future studies undertaken will have to include all the taxa mentioned which show anatomical similarities with this *P. pallida* form F 'pillansii'.

SPECIMENS EXAMINED

CAPE.—3118 (Vanhynsdorp): Nardouwsberge, (—DD), *Ellis* 5779+, 5780+. 3119 (Calvinia): Kobe Mts, (—CA), *Ellis* 2440, 2441, 2442; Elizabethfontein, (—CC), *Ellis* 5420+. 3218 (Clanwilliam): Piketberg, Versfeld's Pass, (—DC), *Ellis* 5481, 5482+. 3219 (Wuppertal): Cederberg, Cederberg Pass, (—AC), *Ellis* 5505+; Welbedacht, Sleepad Hut, *Ellis* 5507+; Sneekop Peak, *Ellis* 5509; Helshoogte Pass, *Ellis* 5588*.

* *P. rupestris*-like specimen.

+ specimens with *P. tomentella* type macrohairs.

7g *P. pallida* form G 'silvatica'

pp. 142–144 (Linder & Ellis 1990a: 41)

A rather distinct taxon with soft, lax leaves and copious glands, it occurs on forest margins in the Knysna forest.

The glands of this species are very unusual, being slightly raised and elongated, the sessile elongated type of Linder *et al.* (1990) although they are slightly constricted at the base (Figure 7g.3E). This is the only taxon in *Pentastichis* observed in this study which has this gland type on its leaves, although this sessile elongated type of gland was also observed on the glumes of *P. natalensis*, *P. cirrhulosa* and *P. lima*. These glands are very common on the keels of the glumes of form G and this character alone separates it from all the other entities assigned to *P. pallida*, and suggests affinities with *P. natalensis* and its allies.

Two other species of *Pentastichis* have a superficially similar type of elongated gland located on the ribs on the adaxial surface of the leaf blades. Examples are *P. aurea* subsp. *pilosogluma* (Figures 40b.1D, F, G; 40b.3D) and *P. borussica* (Figure 21.1A, B). However, these adaxial elongated glands differ structurally from those of 'silvatica' in that no subglandular cells are present.

Notwithstanding this unique gland type, several other anatomical characters indicate affinity to *P. pallida*, rather than to *P. natalensis*. The general structure and organization of the leaves of 'silvatica' resemble *P. pallida* form

D 'australis' most closely, viz. fusiform long cell shape and absence of abaxial stomata, although the latter character is also shared with *P. natalensis*. Macrohair structure suggests affinities with *P. pallida* form B and the other taxa sharing the cushion-based hair type with thickened walls and a constricted hair base: *P. patula* and *P. veneta*.

The anatomy indicates that the relationships of *P. pallida* form G are contradictory and confusing. Nevertheless, it does not appear to be correctly placed here in *P. pallida* and the unique gland type and habitat suggests that this taxon deserves recognition as a separate species, perhaps in the same group as *P. natalensis*.

However, the habitat of this form is unique within the genus and this may account for the unusual combination of anatomical characters exhibited. Specializations for a moist semi-shade environment have undoubtedly occurred in this form and similarities with other taxa may be the result of convergence. It is of interest to note that this taxon appears to be regularly infected by fungi (Figure 7g.2C, D, E) and is perhaps not very well adapted to this cool, moist habitat. Similar fungal infections sometimes occur in other species from cooler, misty habitats such as *P. veneta* (Figure 1.2F). It may be significant that the hyphae were always noted on the macrohairs in both these taxa.

SPECIMENS EXAMINED

CAPE.—3322 (Oudtshoorn): George Dist., Kraalbos, Kaaimans River valley, (—DC), *Ellis* 5599, 5600, 5819, 5820, 3323 (Willowmore): Knysna Dist., Buffelsnek Forest, (—CC), *Ellis* 5831.

8 *P. densifolia* (Nees) Stapf

pp. 145–147 (Linder & Ellis 1990a: 41)

This cushion-forming species has a distinctive habit and is found in specialized montane habitats on rock ledges, crevices, and flushes, often growing in moss beds. The habitat of *P. densifolia* is therefore, essentially one of extremes of temperature, insolation, radiation and water availability.

Virtually all other *Pentastichis* species sharing this habitat have acicular leaves and are eglandular, belonging to Groups 2–6. It was expected that *P. densifolia* would also exhibit similar anatomical specializations to this harsh environment. Usually the glandular *Pentastichis* plants of Group 1 from higher altitudes display xerophytic features, such as narrower, thicker inrolled or infolded leaves, increased formation of structural tissue with a tendency to fusion of the abaxial girders. Associated with this is the loss of the abaxial epidermal zonation and stomata may be absent on this surface.

The leaf blade anatomy of *P. densifolia* is surprisingly typical of the mesic type found at lower, more equable climates. The leaf blades, although rather narrow, are open and expanded (Figure 8.1A, C), the cuticle is usually not thickened (Figure 8.1B, E, H) and the abaxial sclerenchyma girders are not broadly trapezoidal or fused (Figure 8.1 E, F). Abaxial stomata and costal and intercostal zones are always present (Figure 8.2). None of these features

suggest adaptation to extremes of temperature or water availability and does not help explain its ability to survive in this alpine environment. Apart from some of the high altitude plants of *P. veneta* and *P. pallida*, with their obvious anatomical specializations (Figure 7b.8), *P. densifolia* is the only species of Group 1 found in the higher mountains yet it exhibits no obvious anatomical adaptations to this habitat.

P. densifolia very commonly has stalked glands on the leaf margins (Figures 8.1A, B, E, F; 8.2A, B; 8.3A, E, D, H) as well as the abaxial surface (Figure 8.1H; 8.3A). The presence of multicellular glands is consistent with the mesic type of leaf anatomy which occurs throughout Group 1 where *P. densifolia* is currently placed.

The mesic anatomy, leaf glands, macrohairs and microhairs all support the placement of *P. densifolia* in Group 1, and in particular Group 1B. The transectional and epidermal anatomy both are very similar to that of *P. veneta* (Figures 1.1–1.3) and *P. pallida* form B (Figures 7b.4; 7b.5). The hexagonal shape of the rather short intercostal long cells is rather unusual and serves to distinguish *P. densifolia* from these taxa. Elongated fusiform long cells without abaxial stomata distinguish *P. pallida* form D (Figure 7d.2) and form G (Figure 7g.2). The short hexagonal type of long cell sometimes occurs in *P. pallida* form B and form F (Figure 7f.3B, H).

The study sample displayed very homogeneous anatomy except for a few specimens which tend to *P. pallida* form F in anatomy as illustrated in Figures 8.1G and 8.2B. Robbertse (1959) also illustrates this type of anatomy under *P. densifolia*. These specimens have thicker leaves, wider girders, a thicker cuticle and rectangular long cells with sinuous walls. Glands may be rare or absent. These specimens are also morphologically not typical *P. densifolia* and do not have the characteristic pink, older leaves. These plants colonize sandy soil between rock after fire—an unusual habitat for *P. densifolia*.

P. densifolia, therefore, appears to be correctly classified with the Group 1 species and shows firm links to *P. pallida* form B as well as *P. veneta*. Specimens of the high altitude forms of *P. pallida*, which may be morphologically difficult to distinguish from *P. densifolia*, are anatomically quite distinct, and may be better accommodated in *P. pallida* form F in particular. However, this latter taxon is in itself a very variable entity showing links to several other taxa and is not entirely satisfactory as constituted here.

SPECIMENS EXAMINED

CAPE.—3219 (Wuppertal); Cederberg, Sneekop Peak, (—AC), *Ellis* 5519; Middelberg North Peak, *Ellis* 5584; Citrusdal, Middelberg Mts, (—CA), *Ellis* 2493. 3319 (Worcester); Hex River Mts, Milner Peak, (—AD), *Ellis* 5527; Du Toitskloof Pass, (—CC), *Ellis* 5977; Riviersonderend Mts, Jonas Kop, (—DC), *Ellis* 4687. 3321 (Ladismith); Groot Swartberg, W of Waboomsberg, (—BD), *Ellis* 5621. 3419 (Caledon); Riviersonderend Mts, Die Galg, (—BA), *Ellis* 5559.

9 *P. cirrhulosa* (Nees) Linder

pp. 148–150 (Linder & Ellis 1990a: 42)

The anatomical sample used in this study is restricted to specimens from humic soil pockets on limestone rock in the De Hoop area. However, *P. cirrhulosa* is widespread in the southern Cape Province, from Swellendam to Humansdorp and inland to Oudtshoorn, where it is often associated with conglomerates. This anatomical study may, therefore, apply only to the limestone ecotype of this species and additional collections of this very interesting species are required.

The anatomy of the *P. cirrhulosa* specimens studied does not conform closely to that of the mesic type which is characteristic of all the glandular species of Group 1. Instead it resembles that of most of the sclerophyllous leaved species of Groups 3–6, all of which are eglandular. The sclerophyllous leaf type is typically permanently inrolled and filiform or acicular, with no abaxial stomata and very compact mesophyll of small isodiametric cells with minute intercellular air spaces. Sclerenchyma tissue is abundant and adjacent abaxial girders often merge, forming a continuous hypodermal fibrous layer. Epidermal zonation is thus often not differentiated. This anatomical type is fully discussed in the introduction.

The only anatomical indication that *P. cirrhulosa* may in fact belong to the mesic type is in the mesophyll, where the chlorenchyma cells, although compactly arranged, are not angular and isodiametric, particularly those located nearer the adaxial surface (Figure 9.1D). Air spaces are therefore visible, which is not the case in the typical sclerophyllous leaf type.

Several eglandular *Pentastichis* species also have this type of mesophyll which does not strictly conform to the definition of the sclerophyllous type of anatomy. Examples are *P. calcicola* (Figures 45a.1A, B; 45b.1B, D), *P. montana* (Figure 46.1) and *P. rigidissima* (Figure 47.2) as well as *P. chippindalliae* (Figure 53.1), *P. exserta* (Figure 54.1) and *P. basutorum* (Figure 55.1) from the summer rainfall region. *P. lima*, a glandular species of Group 1B also has this type of anomalous anatomy (Figures 11.1; 11.2). In all these species the mesophyll does not consist of compact isodiametric cells, but rather of compact rounded or inflated cells as in *P. cirrhulosa* (Figure 9.1).

On anatomical grounds alone, *P. calcicola*, *P. rigidissima* and *P. cirrhulosa* share many similarities. However, none of these other species has glands anywhere on the plant, whereas stalked, crateriform glands are common on the leaf-sheaths, glumes and, in particular, the pedicels of *P. cirrhulosa*. They are absent on the leaf blades, however. On the basis of the presence of stalked glands, the affinities of *P. cirrhulosa* appear to lie with the *P. pallida* complex but this is not supported by the anatomical evidence.

The overall similarity in leaf anatomy between *P. cirrhulosa* and *P. calcicola* var. *calcicola* in particular, is striking. This includes the abaxial epidermal configuration

as a comparison of Figures 9.2 and 45a.2 clearly shows. It may be coincidental that all the specimens of *P. cirrhulosa* studied, as well as *P. calcicola*, originated in the limestone soils of the Bredasdorp District. The similarity in anatomy may consequently result from convergence in response to this very distinct habitat.

In addition to the sclerophyllous features, there are several other anatomical attributes of *P. cirrhulosa* that are unusual for Group 1. Examples are the complete absence of abaxial epidermal appendages (Figure 9.2), the inflated microhair distal cell (Figure 9.3C) and the larger size of the abaxial epidermal cells as compared to the adaxial ones (Figure 9.1). All these features are sometimes found in representatives of the eglandular species groups but are unknown in Group 1. Many sclerophyllous taxa are without abaxial appendages particularly macrohairs and microhairs. Short microhairs with wide distal cells are rare in *Pentastichis* but are sometimes found in *P. argentea* of Group 2A (Figure 32.4A), *P. colorata* (Figure 41.5B,F) and *P. malouinensis* (Figure 48.3B) of Group 3A, *P. exserta* of Group 3B (Figure 54.3B,C) as well as the *Merxmüllera stricta* complex. Larger abaxial epidermal cells also occur on *P. colorata* (Figure 41.2) and *P. tortuosa* (Figure 42.1) as well as *P. tysonii* (Figure 51.1). This difference between epidermal cell size is also typical of the anatomy of *Pseudopentameris* (Ellis 1985a) and *Pentameris* (Ellis 1985b, c, d).

P. cirrhulosa and *P. lima* are the only known examples where the correlation between mesic anatomy and the possession of multicellular glands breaks down. No other examples are known with sclerophyllous anatomy and stalked glands. However, the mesophyll tissue of both these anomalous species is not entirely consistent with that of the sclerophyllous type and they may be incorrectly categorised as such.

On the anatomical evidence available to date, *P. cirrhulosa* appears to be truly intermediate between these two major evolutionary lines in the genus. This may imply that they are not as phylogenetically important as initially thought, or, otherwise the circumscription of these two anatomical types is not sufficiently detailed to ensure their separation. *P. cirrhulosa* is undoubtedly vital to a more complete understanding of these two basic anatomical types and additional material from new localities is needed for this purpose.

The dark granular inclusions in all or most of the abaxial epidermal cells of all the specimens studied are of particular interest (Figures 9.1A,C,D; 9.2). These conform in all respects to the tannin-like epidermal cells which are common in tropical Andropogoneae and Arundinelleae (Ellis 1990). This type of epidermal cell is not known in C_3 grasses except for two species of *Ehrharta*—*E. dura* and *E. microlaena* (Gibbs Russell & Ellis 1988). *P. cirrhulosa* is therefore, only the third C_3 species reported to possess these cells in the Arundinoideae.

SPECIMENS EXAMINED

CAPE.—3420 (Bredasdorp): De Hoop Nature Reserve, (—AD), Ellis 2524, 4664; between De Hoop and Arniston, (—CB), Ellis 2531.

10 *P. tomentella* Stapf

pp. 151–155 (Linder & Ellis 1990a: 43)

This species is morphologically rather variable, this variation being geographically based. The diagnostic characters of *P. tomentella* tend to break down at the southern end of the distribution range where distinctions with *P. pallida* form F may be difficult to delimit consistently. The anatomical results fully support these morphological indications with the intermediate specimens also coming from the southern parts of Namaqualand.

Typical specimens of *P. tomentella* from Namaqualand have long, flexible macrohairs with slightly swollen bases inserted between one or two inflated epidermal cells (Figure 10.3). This distinctive hair type is also clearly illustrated in Robbertse (1959) under both *P. tomentella* and *P. brachyanthera*. The length of these macrohairs is very variable but the nature of the associated basal cells remain consistent. These hairs are responsible for the grey puberulous or villous nature of the leaf blades—a diagnostic character of this species. However, hairs which are structurally identical, but very much shorter, occur on some specimens of *P. pallida* form F. These specimens do not have a fine grey covering on the leaves and so are not assigned to *P. tomentella* but the shared possession of this unusual hair type strongly suggests that the diagnosis of *P. tomentella* should be widened to include these specimens.

The leaf outlines of *P. tomentella* may be open and expanded or inrolled to varying degrees with the tightly inrolled specimens usually with a much thicker cuticle. These narrower leaves (Figure 10.1D–F) are generally much more xerophytic than the broader, expanded leaves (Figure 10.1A–C) with more supporting tissue and more compact mesophyll. This variation does not appear to have a geographical component and specimens from the same population may exhibit these differences. An example from Aninaus Pass in northern Namaqualand is Ellis 5771 and 5772 (Figure 10.2C, D).

Generally the open, expanded leaf type is associated with long, flexible macrohairs (Figure 10.3A–D), whereas the inrolled leaves tend to have shorter macrohairs (Figure 10.3E–H) although they are still structurally similar. In the southern populations these macrohairs are often so short that the specimens cannot be assigned to *P. tomentella* but are determined as being *P. pallida* form F instead. This is further discussed under the latter species.

P. airoides subsp. *airoides* (Figure 13a.2) and *P. capillaris* (Figure 14.2) also have very similar hairs although the inflated basal cell may not be quite so evident and several additional epidermal cells may be associated with the hair base. Strong links between *P. tomentella* and these latter two annuals of Group 1C are indicated by their overall leaf anatomy.

Glands in *P. tomentella* may be absent on the leaf segments studied, restricted to the margins, or may be present on the margins as well as the abaxial and the adaxial epidermides. The latter condition (Figure 10.2) is unusual but is shared with a few representatives of several

other species of Groups 1A and B. These specimens all come from the area of sympatry of *P. tomentella* and these other taxa viz. from the Cederberg to Nieuwoudtville but the adaxial glands also occur further northwards on *P. tomentella*. Some of the specimens of the other taxa which possess this gland type do not share the same macrohair type which makes the evaluation of both these characters very circumspect. Examples are: (i) *P. veneta* (Figure 1.II, J) where adaxial glands are very rare and macrohairs are absent; (ii) *P. barbata* subsp. *barbata* (Figures 2a.7A, B; 2a.8D, F) where adaxial glands but no macrohairs occur on the northern strandveld form from the St Helena Bay area; (iii) *P. pallida* form F (Figures 7f.2E, F; 7f.4G, H) from the Cederberg which shares the same macrohairs with *P. tomentella*.

These *P. pallida* form F specimens with adaxial glands and macrohairs, therefore, appear to be anatomically identical and could be better assigned to *P. tomentella*. This will necessitate a broadening of the deliniation of *P. tomentella* to accommodate these specimens which do not possess a visible pubescence on the leaf blades.

SPECIMENS EXAMINED

CAPE.—2917 (Springbok): Steinkopf Dist., summit of Aninaus Pass, (—BA), *Ellis* 5080; base of Aninaus Pass, (—BC), *Ellis* 5771, 5772; Springbok Dist., Modderfontein, (—DA), *Van der Westhuizen* 315; Spektakel Pass, *Ellis* 5392, 5393; O'Kiep, (—DB), *Ellis* 2143, 2144. 3017 (Hondeklip Bay): 52km S of Springbok, (—BB), *Ellis* 2198, 2199. 3119 (Calvinia): top of Vanrhyn's Pass, (—AC), *Ellis* 1141, 2458, Nieuwoudtville Dist., Noord-Bokkeveld, Kleinplaas, *Ellis* 5774, 5775.

11 *P. lima* (Nees) Stapf

pp. 155–157 (Linder & Ellis 1990a: 44)

This rare, localized Kamiesberg endemic possesses an unusual combination of characters in that it has conspicuous glands on the pedicels and glumes but has rolled, setaceous leaves.

The leaf anatomy corresponds to the sclerophyllous type in all respects, except the mesophyll which is clearly not comprised of small, compact isodiametric chlorenchyma cells, as is typical of the sclerophyllous type. Instead the chlorenchyma cells are angular but large (considerably larger than the parenchyma sheath cells) and very irregularly arranged with large intercellular air spaces (Figure 11.ID). This is typical of the mesic type of anatomy, as discussed in the introduction. It is therefore assumed that this is a highly modified example of the mesic type.

In *Pentastichis* the mesic type of the Group 1 taxa is strongly correlated with the occurrence of glands but this type of modification of the mesic type (closely resembling the sclerophyllous type) makes interpretation of homologies difficult. A single similar exception is known. *P. cirrhulosa* (Figures 9.1; 9.2; 9.3), where the interpretation of the leaf anatomy proved to be unsatisfactory as no precedents were available of the possible extremes of modification of the basic mesic leaf type. The specialized high altitude plants of *P. pallida* form B (Figure 7b.8) give some indication of the degree of modification that is possible. *P. lima* will undoubtedly contribute to our knowledge of the interface between the mesic and the

sclerophyllous leaf types which so conveniently divide the genus into two major groups and are correlated with the glandular and eglandular species groups.

Several eglandular species have similar anomalous sclerophyllous leaf blade anatomy, examples being *P. calcicola* (Figures 45a.1A, B; 45b.1B, D), *P. montana* (Figure 46.1) and *P. rigidissima* (Figure 47.2) in addition to *P. chippindalliae*, *P. exserta* and *P. basutorum* from the summer rainfall region of southern Africa. Conclusive evidence that glands have been secondarily lost in some or all of these taxa will facilitate the interpretation of the unusual anatomical type exhibited by *P. lima*.

The leaves of *P. lima* are noticeably scaberulous due to the presence of the numerous abaxial hooks located throughout the epidermis—which is unique in the genus. In fact, at first glance, the epidermis, and leaf transverse sections, of *P. lima* closely resembles that of many *Festuca* species but the presence of microhairs (Figures 11.2D; 11.3B, E, F) refutes possible pooid affinities.

The relationships of *P. lima* are therefore, obscure and it appears to be truly intermediate between the glandular *Pentastichis* species of Groups 1 and 2 and the eglandular species of Groups 3–6. Further studies on this poorly known species are required to help elucidate the phylogeny of the genus.

SPECIMENS EXAMINED

CAPE.—3018 (Kamiesberg): Leliefontein Dist., Kamiesberg, (—AB), *Ellis* 5995, 5996, Eselkop, *Ellis* 5998.

Group 1C

This group includes all the glandular species which have stalked glands and are annual in habit. Some weakly perennial taxa may also be included.

Most of these annuals display strong anatomical links to perennial species of other Group 1 subgroups. Consequently, this group does not appear to be a natural phylogenetical grouping, and the annual habit seems to have arisen independently several times. Group 1C can be conceived as being one extreme of a morphological cline which accommodates all the weakly perennial and annual taxa possessing glands. Thus several similar anatomical trends are evident which transect Groups 1A, B and C.

Some of the Group 1C taxa are without foliar glands (*P. patula* form A, *P. aristifolia*) and their overall leaf anatomy resembles that of some perennial species of Groups 1D and E (*P. microphylla*, *P. ecklonii*, *P. reflexa*) as well as some specimens of *P. pallida* forms A and F of Group 1B.

The glandular species of Group 1C also appear to belong to two different groups each linked to perennial species of other species groups: (i) species with stiff, cushion-based macrohairs (*P. patula* form C) for which affinities with *P. pallida* form B and its allies are indicated; (ii) species with slender, flexible macrohairs associated with

only a few inflated epidermal cells tending to resemble either *P. tomentella* (*P. airoides* subsp. *airoides*, *P. capillaris*) or *P. galpinii* and *P. oreodoxa* (*P. airoides* subsp. *jugorum*).

Group 1C, therefore, appears to be polyphyletic including all the glandular annual species which have adopted a similar habit probably in response to drier habitats or richer soils. These taxa are very rare on Table Mountain Sandstone derived quartzitic sands. They are, therefore, more common away from the heartland of the fynbos biome, especially on the arid more northern fringes of the winter rainfall region of the Cape Province.

Species delimitations are also somewhat arbitrary in some of the taxa of this subgroup with excessive anatomical and morphological ranges of variation. The recognition of this infrageneric grouping may be an oversimplification and the *P. patula*–*P. pallida* complex, in particular, may have to be revised. Nevertheless, this subdivision is convenient for herbarium identification purposes even if it does not represent natural phylogenetic lineages.

12 *P. patula* (Nees) Stapf (Linder & Ellis 1990a: 45)

A strictly annual species which is widespread in the south-western Cape, ranging from Namaqualand southwards to Worcester, *P. patula* is distinguished from *P. airoides* by larger anthers and a stronger growth form. Anatomically these two superficially similar species can be separated by their different macrohairs—when present on *P. patula* form C ‘heteroplo’, they are thick, stiff hairs embedded in a raised cushion base, whereas those of *P. airoides* are thin and flexible and are associated with only a few inflated epidermal cells at the base. However, *P. patula* form A ‘patula’ is without macrohairs and resembles *P. aristifolia* in anatomy.

P. patula is morphologically very variable and is informally separated into three forms. Further studies may lead to their recognition at the specific level as there is close congruence between the anatomical and morphological evidence separating these informal forms.

12a *P. patula* form A ‘patula’ pp. 158–160 (Linder & Ellis 1990a: 46)

This is a stiff, erect, glabrous form which occurs north of Clanwilliam. The plants resemble *P. aristifolia* closely and they are both glandular. However, no aristae are present on the leaves of *P. patula* form A. The anatomy indicates that this form is indeed very close to *P. aristifolia*. If the aristae are not considered to be diagnostic of *P. aristifolia*, then this form of *P. patula* would be included in *P. aristifolia*. However, as presently constituted, these two taxa utilize different substrates with this form occurring in Namaqualand, whereas *P. aristifolia* is a Karoo endemic.

This form of *P. patula* is anatomically very similar to *P. aristifolia* and they cannot be distinguished on

anatomical criteria. Both are without glands and macrohairs on the leaf blades, their epidermal patterns cannot be distinguished and both have distinctive small costal prickles, sinuous long cell walls, conspicuous stomata and clearly differentiated costal zones with irregularly dumbbell-shaped silica bodies (Figures 12a.2; 15.1C–F). In cross section both taxa have medium adaxial ribs and furrows with well-developed adaxial sclerenchyma strands present in the ribs (Figures 12a.1; 15A, B). These are considerably larger than the abaxial strands, a very unusual configuration in grasses.

The chlorenchyma of both taxa is of particular interest in that it closely resembles the unusual type described in *Chaetobromus* (Ellis 1988b) which possibly represents a new photosynthetic type in the Poaceae, possibly equivalent to the CAM photosynthetic pathway. The lateral cell count is rather low, the cellular arrangement tends to the radial type and the chloroplasts are refractive under interference contrast illumination (Figure 12a.1D). This unusual photosynthetic anatomy occurs in several other arundinoid grasses which also occur in the succulent karoo biome. Examples are *Chaetobromus*, *Dregeochloa* (Ellis 1977), *Merxmüllera rangei* (Ellis 1982b) and several species of *Ehrharta*. This chlorenchyma modification, therefore, appears to be an adaptation to the specific environmental conditions of this region which is dominated by succulents. The functional significance of this chlorenchyma type deserves further study.

P. patula form C, on the other hand, differs in several significant respects from form A which suggests that these two taxa are not closely allied. The anatomical differences include the presence of glands, macrohairs and the normal mesic type of chlorenchyma in *P. patula* form C (Figures 12c.1; 12c.2). Whereas form A shows strong links to *P. aristifolia*, *P. microphylla*, *P. ecklonii* and *P. reflexa* in addition to *P. pallida* form A, the affinities of form C appear to lie with *P. pallida* form B and its allies such as *P. densifolia*, *P. barbata* (Montane form) and some specimens included in *P. rupestris* and *P. veneta*.

P. patula form A, therefore, is consistently distinct in leaf anatomy from form C and these two forms seem to have different affinities and origins. This strongly suggests that they should be separated at the specific level as no intermediates were observed in the sample studied. However, no material of *P. patula* form B ‘euadenia’ was examined in this study and, until this is done, no firm recommendations can be made.

SPECIMENS EXAMINED

CAPE. —3118 (Vanrhynsdorp): Nardouskloof, (–DD), Ellis 5781. 3119 (Calvinia): Doring River between Calvinia and Clanwilliam, (–CC), Ellis 5418.

12b *P. patula* form B ‘euadenia’ (Linder & Ellis 1990a: 46)

No anatomical material of this form was examined in this study. It is only known from the Kamiesberg and has been poorly collected and insufficiently studied. Material of this form is needed in order to gain a better under-

standing of the relationships between the three forms of *P. patula*. No intermediates between forms A and C have been found but 'euadenia' may represent this link.

12c *P. patula* form C 'heteroplo'

pp. 161–163 (Linder & Ellis 1990a: 47)

This is the most common and widespread form of *P. patula*, extending southwards from Nieuwoudtville to Worcester. It is a softly hairy, decumbent plant that often forms sprawling mats in physically disturbed habitats, particularly in more arid areas.

It has typically mesic anatomy with diffuse mesophyll without a continuous abaxial cuticle (Figure 12c.1). The epidermis is clearly differentiated into narrow costal and wider intercostal zones with elongated, slightly sinuous, thin-walled intercostal long cells and abaxial stomata. The costal zones have irregularly dumbbell-shaped silica bodies, sometimes tending to the nodular type (Figure 12c.2). Although this species occurs in arid habitats there are no apparent xerophytic adaptations evident in the leaf anatomy. This species is, therefore, essentially a short-lived ephemeral relying entirely on sufficient sporadic rainfall for its growth requirements.

Leaf glands do occur but are not very common (Figures 12.1C; 12c.2A; 12c.3D). The glands are restricted to the leaf margins and only have short stalks. This gland structure differs considerably from that of the morphologically similar *P. airoides* where glands with elongated stalks are relatively common (Figures 13a.1; 13a.3E,D,H).

The macrohairs of *P. patula* form C and those of *P. airoides* also differ substantially. These hairs in *P. patula* 'heteroplo' are stiff, with thickened walls and the constricted base is embedded in a raised cushion of numerous specialized epidermal cells (Figures 12c.2; 12c.3A, C). The macrohairs of *P. airoides*, on the other hand, are usually soft, thin and flexible and are only associated with one or two inflated epidermal cells (Figure 13a.2). The leaf anatomy indicates, therefore, that *P. patula* form C and *P. airoides* are not closely related, notwithstanding their superficial morphological resemblance and habit.

The macrohair type present on *P. patula* form C may indicate affinities with other taxa sharing this type of macrohair. Examples are *P. veneta* (Figure 1.2B) and *P. pallida* form B (Figures 7b.4C, D; 7b.5). Strong links with *P. pallida* form B are suggested by the overall leaf anatomy. This relationship with *P. pallida* appears to be much stronger than that to *P. patula* form A as discussed under the latter taxon. In fact the anatomy suggests that *P. patula* form C can be considered to be an annual form of *P. pallida* form B which is strictly a weak perennial. The separation of these two taxa may be somewhat arbitrary along an environmental gradient. Both also have anthers of similar size, being much larger than those of *P. airoides*.

SPECIMENS EXAMINED

CAPE.—3017 (Hondekliptaai): between Kotzesrus and Groen River mouth, (—DC), *Ellis* 5412. 3118 (Vanrhynsdorp): between Elizabeth-

fontein and Nardouskloof, (—DD), *Ellis* 5424. 3119 (Calvinia): Kobe Mts, (—CA), *Ellis* 2438, 2443. 3217 (Vredenburg): Paternoster, (—DD), *Ellis* 5133. 3219 (Wuppertal): Pakhuis Pass, (—AA), *Ellis* 1165. 3220 (Sutherland): Verlatekloof, (—DA), *Ellis* 6000.

13 *P. airoides* (Nees) Stapf

(Linder & Ellis 1990a: 47)

P. airoides is a widespread annual in the winter rainfall region particularly in the lowland Renosterveld areas on richer soils, although it occasionally occurs on Table Mountain Sandstone derived sands as well. *P. airoides* extends into the summer rainfall area of South Africa. The plants from these two climatic regions differ morphologically and are recognised as separate subspecies.

The more robust forms of *P. airoides* are superficially difficult to distinguish from *P. patula* form C and *P. pallida* form B, but the minute anthers provide a constant key character as do the glands and macrohairs. The glands of *P. airoides* have much more elongated stalks than do those of *P. patula* form C. The macrohairs of *P. patula* 'heteroplo' are stiff with a constricted base embedded in a raised cushion of numerous specialized epidermal cells. This structure differs from the hair type of *P. airoides* where thin, soft, flexible macrohairs are associated with only one or two inflated epidermal cells.

13a *P. airoides* (Nees) Stapf subsp. *airoides*

pp. 164–167 (Linder & Ellis 1990a: 48)

This subspecies includes all the plants from the winter rainfall area, generally from richer soils but it may occur on Table Mountain Sandstone derived soils. This form occurs in a wide range of vegetation types, from fynbos to Renosterveld and even semi-desert. The plants tend to be small, with few culms and with a relatively large, open inflorescence.

The anatomy of the very soft, expanded leaves is characterized by a very diffuse mesophyll, slight adaxial ribbing and a thin discontinuous cuticle (Figure 13a.1). As in *P. patula* form C there is no evidence of anatomical xerophytic adaptation. Both taxa have a very rapid life cycle, growing when moisture is available.

Long-stalked glands are very frequent on the leaf margins (Figures 13a.1B–D; 13a.3E, D, H) and these differ structurally from the morphologically similar *P. patula* form C in having elongated stalks. The glands appear to be identical to those of *P. capillaris* (Figures 14.1C, D; 14.2A).

The structure of the very common macrohairs also serves to separate *P. airoides* from the superficially similar *P. patula* form C. Both *P. capillaris* and *P. airoides* have thin and flexible macrohairs with a slightly swollen base inserted between two inflated and structurally modified epidermal cells (Figure 13a.2). Other species which possess this kind of macrohair are *P. tomentella* (Figure 10.3) and sometimes *P. pallida* form F (Figure 7f.3). Basically similar hairs also occur on *P. oreodoxa* (Figure 23.3) and some specimens of *P. setifolia* (Figure 24.2),

but in these latter species the hairs are thicker and stiffer and resemble those of *P. airoides* subsp. *jugorum* closely (Figure 13b.2D).

The leaf anatomy indicates, therefore, that *P. airoides* subsp. *airoides* is closer to *P. capillaris* and *P. tomentella* (and their allies) than it is to subsp. *jugorum*. Once again the anatomical characters cut across the subgroups of Group 1 rather than remaining consistent within them and the annual-perennial dichotomy does not seem to be supported by the leaf anatomy. However, this observation is not corroborated by anther size which consistently separates *P. airoides* from these other taxa.

Awn length in *P. airoides* subsp. *airoides* is very variable, with some specimens having very short awns. An example is *Ellis 5120* in which the awns are barely exerted beyond the glumes. However, the leaf anatomy conforms to that of *P. airoides* subsp. *airoides* in all respects and the reduction in awn length in this taxon seems to have no taxonomic importance.

Microhairs in *P. airoides* subsp. *airoides* are typically finger-like with the two cells about equal in length. Occasionally abnormal tricellular microhairs were observed (Figure 13a.3B). This unusual configuration is not unique in subsp. *airoides* and has also been noted in *P. rupestris* (Figure 5.3C), *P. pallida* form F (Figure 7g.5D) and *P. pallida* form G (Figure 7g.2F). No taxonomic importance is attached to this rare deformity.

SPECIMENS EXAMINED

NAMIBIA.—2616 (Aus): Aus, (—CB), *Ellis 5066*.

CAPE.—2917 (Springbok): Aninaus Pass, (—BA), *Ellis 5082*; Spektakel Pass, (—DA), *Ellis 5394*; Springbok, (—DB), *Ellis 2156*, 3017 (Hondeklip Bay): Killian's Pass, (—BA), *Ellis 2149*; Kamieskroon, (—BC), *Ellis 5096*, 3218 (Clanwilliam): Pakhuis Pass, (—BB), *Ellis 1702*; Versfeld's Pass, (—DD), *Ellis 5125*, 5126, 3219 (Wuppertal): Op-die-Berg, (—CD), *Ellis 5120*, 5121, 3220 (Sutherland): Sutherland, (—BC), *Ellis 5112*, 3321 (Ladismith): Swartberg Mts, Gamkaskloof, (—BD), *Ellis 5632*, 3322 (Oudtshoorn): Outeniqua Mts, Robinson Pass, (—CC), *Ellis 2555*, 3323 (Willowmore): Uniondale Poort, (—CA), *Ellis 1633*, 3421 (Riversdal): Herbertsdale Dist., Cloete's Pass, (—BB), *Ellis 636*.

13b *P. airoides* (Nees) Stapf subsp. *jugorum* (Stapf) Linder pp. 167–169 (Linder & Ellis 1990a: 48)

This subspecies occurs in summer rainfall areas, from the Drakensberg southwards to the Katberg and westwards as far as Bloemfontein. It occurs in shallow sandstone derived soils, often on rock mats, in montane and alpine grassland. Many flowering culms are formed throughout the extended summer rainy season and the plants thus form a stout base. Nevertheless it is doubtful that they are perennial. The inflorescences are also narrower than in subsp. *airoides*.

The epidermal anatomy of this subspecies of *P. airoides* bears an overall resemblance to that of several perennial *Pentastichis* species also from the summer rainfall region of South Africa viz. *P. galpinii* (Figure 17.2), *P. oreodoxa* (Figure 23.3) and the *P. setifolia* specimens without sunken glands (Figure 24.2). The zonation is similar (except

where a hypodermal sclerenchyma layer is present in some specimens of the latter two species), the long cells have sinuous walls with a high frequency of deep undulations, and the silica body shape and arrangement is comparable. The macrohairs (although sometimes very rare) are rather stiff and are inserted between a few inflated epidermal cells and are most frequent laterally on the lamina. In transection all these taxa are also similar except that the leaves of subsp. *jugorum* are narrower and thinner as is to be expected in an annual with short-lived leaf blades.

Short-stalked marginal and unstalked abaxial glands may occur in all these taxa. These abaxial glands may even occur along the midrib (Figure 13b.1F) as shown by Robbertse (1959). The glands of subsp. *jugorum*, *P. galpinii*, *P. oreodoxa* and *P. setifolia* always have concave surfaces (Figures 13b.3D, H; 17.3C, F).

This anatomical structure differs from that of *P. airoides* subsp. *airoides* in several respects. The macrohairs are basically similar except that those of subsp. *jugorum* tend to be shorter and stiffer and are concentrated near the leaf margin. It is of interest to note that the macrohairs of a specimen collected near Trompsburg in the False Upper Karroo (*Ellis 5814*) are very long and thin, closely resembling those of subsp. *airoides*. The shorter, stiffer macrohairs (Figure 13b.2D) are more typical of specimens from alpine habitats further to the east. Macrohair structure, therefore, does not appear to be useful in separating these two subspecies and apparently varies with habitat. *P. airoides* subsp. *jugorum* specimens from the drier west and south generally are anatomically closer to subsp. *airoides* than are the specimens from the wetter eastern mountains.

The glands of these two subspecies are also similar but those of subsp. *jugorum* have very pronounced concave heads and shorter stalks (Figure 13b.3D, H). In subsp. *airoides* glands are restricted to the leaf margin and do not occur abaxially as is the case in subsp. *jugorum*. This difference in gland location appears to be significant taxonomically.

Other anatomical attributes, such as epidermal zonation, long cell shape and wall sinuosity and microhairs show much greater differences, however. The basal cell of the abaxial microhairs of subsp. *jugorum* is longer than the distal cell (Figure 13b.3C, G)—a trend which is further developed in *P. galpinii*, *P. oreodoxa* and *P. setifolia* where this distal cell is very reduced. This distinctive type of microhair does not occur on any other representative of Groups 1A, B or C except *P. papillosa* (Figure 4.3B, C, F, G). The microhair structure of subsp. *jugorum* is intermediate between these two distinctive microhair types.

The anatomical evidence, therefore, does not indicate close affinities between subsp. *airoides* and subsp. *jugorum* but rather that each of these two subspecies is allied to a different group of perennial species belonging to different species groups—Groups 1A, B and C for subsp. *airoides* and Groups 1D and F for subsp. *jugorum*. Nevertheless the separation of these two subspecies is difficult, particularly specimens from the extremes of their respective distribution ranges.

SPECIMENS EXAMINED

O.F.S.—2828 (Bethlehem): Golden Gate Highlands Nat. Park, Brandwag Kop, (—DA), *Ellis* 2364, 2366, 2375, 2376, 3025 (Colesberg); Trompsburg, (—BB), *Ellis* 5814.

CAPE.—3028 (Matatiele): Naudesnek Pass, (—CA), *Ellis* 5680, 5695.

14 *P. capillaris* (Thunb.) McLean

pp. 170–172 (Linder & Ellis 1990a: 48)

A rather robust, glandular annual which is distinguished from all the other species of Group 1 by its lack of awns, it is a rare species endemic to the sandy coastal plains north of Saldanha Bay.

Anatomically *P. capillaris* resembles *P. airoides* subsp. *airoides* closely, especially in transectional anatomy with the very diffuse mesophyll tissue, the abrupt margins, small sclerenchyma girders and the stalked clavate marginal glands of the two taxa being very similar indeed as Figures 13a.1 and 14.1 clearly show. The only differences visible are that the glands in *P. capillaris* are distinctly crateriform (Figure 14.1C; 14.3C, F), a condition not noted in *P. airoides* subsp. *airoides*. The leaves of *P. capillaris* also tend to be somewhat thicker.

The epidermal anatomy of these two taxa is also virtually identical (Figures 13a.2; 14.2). The macrohairs in particular suggest close affinities with *P. airoides* subsp. *airoides* and its relatives such as *P. tomentella*. This slender macrohair type with its insertion between two rounded epidermal cells differs structurally from that of most other *Pentastichis* species; they are always very numerous on the leaves and sheaths of *P. capillaris* and are responsible for the villous nature of these organs.

Thus, although *P. capillaris* is without awns, whereas *P. airoides* subsp. *airoides* and all other glandular species possess awns, the anatomy confirms their classification in a single subgeneric group. The loss of awns appears to have occurred independently several times in the genus and is taxonomically useful only for delimitation of species. In *P. airoides* subsp. *airoides* this reduction in awn length is evident and this supports the anatomical indications that these two taxa are very closely related.

SPECIMENS EXAMINED

CAPE.—3017 (Hondeklipbaai): Kotzesrus, (—DC), *Ellis* 5410, 5411, 3118 (Vanrhynsdorp): between Elizabethfontein and Nardouskloof (—DD), *Spies* 3412, *Ellis* 5782. 3218 (Clanwilliam): Hopefield, Berg River station, (—CD), *Acocks* 24150, 3219 (Wuppertal): Citrusdal, (—CA), *Ellis* 5994.

15 *P. aristifolia* Schweick.

pp. 173, 174 (Linder & Ellis 1990a: 49)

This annual species is without foliar or inflorescence glands and, therefore, does not strictly belong in Group 1 by definition. However, it is morphologically so similar to *P. airoides* that it has been included in this species group. The slender aristae on the leaf apices characterize this species but it shares minute anthers with *P. airoides*.

As currently defined it is unique in the genus in that it is a Karoo endemic, being confined to the Western Mountain Karoo from Nieuwoudtville to Williston. However, the anatomy indicates that additional specimens from north of Clanwilliam should be included here. These specimens are presently classified under *P. patula* form A (which is also eglandular) as they do not have the leaf aristae.

The leaf anatomy of *P. aristifolia* and *P. patula* form A is very similar. Both are without glands and macrohairs and the cellular arrangement of their epidermides is identical (Figures 12a.2; 15.1C–F). The shortly barbed costal prickles are shared by these two taxa and abaxial microhairs are extremely rare on both taxa. In cross section both have medium adaxial ribs and furrows and rather conspicuous sclerenchyma caps associated with all the vascular bundles (Figures 12a.1; 15.1A, B). Although well developed, this sclerenchyma is very unusual in that it is in the form of strands and does not make contact with the bundle sheaths. The adaxial strands are also considerably larger than the abaxial ones, an unusual configuration. The chlorenchyma of *P. aristifolia* differs slightly from that of *P. patula* form A in that it is less dense and radiate. The unusual mesophyll of *P. patula* form-A is further discussed under that taxon.

The anatomy indicates that *P. aristifolia* and *P. patula* form A occupy a rather isolated position within the genus. Morphologically *P. aristifolia* resembles *P. airoides* very closely but this is not substantiated by the anatomy, as they differ in several major respects. *P. aristifolia* is, therefore, the only annual species of *Pentastichis* without obvious links to a perennial species, even those of the eglandular species groups. The fact that it possesses typical mesic type anatomy supports its retention in Group 1 and the annual habit places it here in Group 1C.

SPECIMENS EXAMINED

CAPE.—3119 (Calvinia): Nieuwoudtville, (—AC), *Ellis* 5414, Lokenburg, *Ellis* 1722. 3220 (Sutherland): Middelpost, (—AB), *Ellis* 2463; Sutherland, (—BC), *Ellis* 5111.

16 *P. trisetoides* (Hochst. ex Steud.) Pilg.

p. 174 (Linder & Ellis 1990a: 50)

No freshly fixed material of this Ethiopian endemic was examined anatomically in this study. The herbarium material available proved unsuitable for adequate reconstitution (Figure 16.1) and the preparations proved unsatisfactory for comparative purposes. The leaves appear to be much thinner than those of the other annual *Pentastichis* species and no macrohairs or glands were visible in the serial transverse sections prepared. Epidermal scrapes failed, probably due to the very thin blades and the poor state of preservation of the material.

P. trisetoides is a glandular annual with minute anthers and, as such, is very similar to *P. airoides*. Freshly fixed material is needed to confirm whether gland and macrohair structure compare favourably with those of *P. airoides*.

ETHIOPIA. —No exact locality, *Schimper* 904.

Group 1D

This is a small group of glandular, perennial, mat-forming species in which the lemma awns are reduced or lost. The leaves are rigid and expanded and this is reflected in the anatomy where the sclerenchyma is in the form of well-developed girders. The costal zones are also wide and the intercostal long cells have moderately sinuous walls. Abaxial epidermal appendages are usually lacking and only microhairs rarely occur. Foliar glands may be present or absent.

Only two summer rainfall species are included in this group, *P. galpinii* and *P. microphylla*. The leaf anatomy generally resembles that of *P. airoides* subsp. *jugorum* although the leaves of subsp. *jugorum* are less rigid, thinner and without as much sclerenchyma tissue. This is to be expected in an annual and on leaf anatomy subsp. *jugorum* appears to be closer to this summer rainfall group rather than to subsp. *airoides* from the winter rainfall biome.

The anatomy indicates that this small species group from the mountains of the summer rainfall region is a natural grouping. The inclusion of *P. airoides* subsp. *jugorum* is indicated but relationships to winter rainfall species are less clear. Phylogenetical links to *P. oreodoxa*, *P. setifolia* and *P. glandulosa* of Group 1F are also suggested by the leaf anatomy. In this way a homogeneous group of summer rainfall taxa may be circumscribed which may also include some of the central African taxa which were not studied in sufficient detail in this study.

17 *P. galpinii* (Stapf) McClean pp. 175–178 (Linder & Ellis 1990a: 51)

A low cushion-forming species with glandular, basally aggregated leaves, *P. galpinii* is a high altitude Drakensberg endemic usually occurring on bare, basaltic soils, often a lithophyte in shallow soils bordering bed rock. It is also common on bare ground in frost hollows and appears to tolerate frost heaving.

As in many high altitude *Pentaschistis* species the anatomy suggests xerophytic adaptations. The leaves are relatively thick with prominent adaxial ribs and narrow, cleft-like furrows, sclerenchyma girders are well developed and the mesophyll is rather dense although still of the diffuse mesic type (Figure 17.1). The epidermis has wide costal zones, sinuous long cells, few stomata and hairs and prickles are absent (Figure 17.2). This suite of characters is commonly associated with species from arid or high altitude habitats and appears to be correlated with reduced moisture availability. In the case of *P. galpinii* this may result from freezing of the soil.

The anatomy of *P. galpinii* indicates a relationship with *P. microphylla* of Group 1D and *P. airoides* subsp. *jugorum*

of Group 1C. These three taxa appear to be particularly closely related with *P. oreodoxa*, *P. setifolia* and *P. glandulosa* of Group 1F being slightly further removed. The basic leaf structure of all these taxa is essentially identical with minor specific differences distinguishing each taxon.

The following characters in combination are diagnostic for *P. galpinii*: the presence of slightly raised glands (both marginal and abaxial), the total absence of macrohairs, discrete, but well-developed abaxial sclerenchyma girders which do not fuse and the distinct epidermal zonation. *P. airoides* subsp. *jugorum* sometimes has macrohairs, *P. microphylla* does not have leaf glands and stomata are common and *P. oreodoxa*, *P. setifolia* and *P. glandulosa* may have macrohairs and/or glands which may be of the sunken type. A continuous hypodermal sclerenchyma layer may also be developed.

The sunken glands of the Group 1F species superficially appear to be distinct (Figures 24.3, 4; 26.1–26.4). However, closer examination of the raised glands of *P. galpinii* in transection show that the stalk cells are actually sunken in a crypt located below the level of the epidermis (Figure 17.1E), thus indicating some similarity to the sunken gland type.

Microhair structure may also be meaningful. The very short distal cells of *P. galpinii* (Figure 17.3B, E) seem to be radically different from those of all the other Group 1 species discussed thusfar. However, the intermediate condition, where the basal cell is somewhat longer than the distal cell occurs in *P. airoides* subsp. *jugorum* (Figure 13b.3C, G). The hair type with a minute distal cell is present on *P. oreodoxa* (Figure 23.4C, F) and *P. glandulosa* (Figure 26.4E, F) with *P. setifolia* (Figure 24.5D, H) being somewhat intermediate. Microhairs with this minute distal cell occur widely in the eglandular *Pentaschistis* species of Groups 3–6 but do not occur elsewhere in the glandular species of Groups 1A–C. This unusual microhair structure suggests that Groups 1D and 1F may be closer to the eglandular species than to the rest of Group 1. However, slight structural (not as narrow) and locational (only adaxially located) differences in the microhairs in the eglandular species suggest that this superficial similarity in the microhairs may be the result of convergence.

SPECIMENS EXAMINED

NATAL. —2828 (Bethlehem): Mont-aux-Sources, Sentinel Peak, (–DB), Ellis 3148, 5728, 5732, Du Toit 659, 660, 663, 668, 2829 (Harrismith): Cathedral Peak, Organ Pipes Pass, (–CC), Ellis 1388, 5720, 2929 (Underberg): Sani Pass, (–CB), Du Toit 2203, 2204, 2283, 2286, 2288, 2289, 2298, Ellis 5704, 5705, 3028 (Matatiele): Naudesnek, (–CA), Ellis 5694.

18 *P. microphylla* (Nees) McClean p. 179 (Linder & Ellis 1990a: 51)

A distinctive cushion-forming species from the Stormsberg and Winterberg of the eastern Cape, it occurs at high altitudes in shallow soils over bedrock and, like *P. galpinii*, can tolerate low temperatures and heavy snowfalls.

This is reflected in the markedly xerophytic nature of the anatomy where the trapezoidal abaxial sclerenchyma girders are particularly prominent (Figure 18.1B, D). The large number of abaxial stomata (Figure 18.1E, F) are not normally associated with species displaying xerophytic adaptations and are in marked contrast to the situation in *P. galpinii* (Figure 17.2) where stomata may be absent or widely spaced. *P. microphylla*, unlike *P. galpinii*, is without foliar glands.

P. microphylla has been poorly collected and its distribution range is imperfectly known. It was only represented in this study by three specimens, all originating from the same population and all being virtually identical in leaf anatomy. Consequently the range of anatomical variation is unknown. Nevertheless the results indicate that *P. microphylla* is very close to *P. galpinii* and its allies and yet can be separated from these taxa by the absence of glands, the very well-developed abaxial girders and the abaxial stomata.

SPECIMENS EXAMINED

CAPE.—3126 (Queenstown): Penhoek Pass, (—BC), Ellis 2592, 2593; Buffelsfontein, Stretton 185.

Group 1E

This is a small, poorly studied group of winter rainfall species with awnless lemmas. Both species included in this group are very rare and localized in their distribution ranges and have been insufficiently collected and studied anatomically. Fresh material of both was collected in the field and the leaf anatomy can be described but no firm conclusions can be drawn as to their relationships.

The leaves of both *P. ecklonii* and *P. reflexa* are expanded and rigid but are unusual in being cauline. Glands do not occur on these leaves but are present on the pedicels and glumes. Anatomically and morphologically these leaves resemble those of the Group 1D species (except that *P. galpinii* has glands) as all these taxa exhibit xeric tendencies. However, this appears to result from convergence rather than indicating close phylogenetic relationships. Thus *P. galpinii* and *P. microphylla* are adapted to alpine or subalpine summer rainfall conditions, whereas both *P. ecklonii* and *P. reflexa* occur in lowland habitats in the fynbos—either sandy or shaley soils on the Cape Flats to the Bredasdorp area or the arid fynbos on the lower slopes of the mountains of the western Cape Province. The Group 1E species are, therefore, adapted to summer droughts, whereas the Group 1D species can withstand frozen soil conditions in the early summer, i.e. xerophilic and cryophilic adaptations which result in anatomically very similar adaptations but may not indicate affinity.

19 *P. ecklonii* (Nees) McClean

pp. 180, 181 (Linder & Ellis 1990a: 52)

P. ecklonii is generally considered to be a Cape Flats endemic occurring on sandy soils but now is very rare due

to urban development. It is unusual in that it flowers very late in the season, during the very dry summer months as late as March.

For this study a single population was located in the Gansbaai area of the Bredasdorp District, thus extending the known distribution further eastwards. It was found growing in fine, grey clayey waterlogged soil overlying laterite, a soil type which is known from its other known provenances where it has been extensively ploughed for agricultural crop production.

The anatomy of *P. ecklonii* is strongly xerophilic with well-developed abaxial sclerenchyma girders evident. These display a tendency to lateral fusion (Figure 19.1A, B) and can form a continuous hypodermal layer. This feature was not reflected in the epidermal structure of the specimens studied as zonation and stomata were evident (Figure 19.1C, D). However, additional collections will probably confirm this xeromorphic trend.

The epidermis is without appendages except for microhairs. These are noteworthy in that the distal cells are usually collapsed and appear to release a secretion which conspicuously stains the surrounding epidermal cell walls. This species may provide useful study material for investigating the functional significance of these microhairs.

The leaf anatomy of *P. ecklonii* bears an overall resemblance to that of *P. reflexa* and these two species appear to be correctly placed in the same species group. They display no unique diagnostic features and links to other subgroups are not clear. The mesic anatomy (together with the pedicel glands) confirms their placement in the glandular Group 1.

SPECIMENS EXAMINED

CAPE.—3419 (Caledon): Bredasdorp Dist., Viljoenshof, (—CA), Ellis 5984, 5985.

20 *P. reflexa* Linder

pp. 181–183 (Linder & Ellis 1990a: 53)

A very rare species from the arid fynbos on the lower slopes of the Cederberg, Piketberg and the Olifants River mountains, it appears to be related to *P. ecklonii* but can be distinguished by its reflexed spikelets and clavate hairs on the lemmas. The leaf anatomy supports this relationship.

Only a single population was sampled for anatomical study, albeit in two different seasons. All plants had glabrous leaves without cushion-based hairs. The leaf blades are expanded (Figure 20.1) or slightly rolled and rather rigid with abaxial and adaxial girders associated with all vascular bundles (Figure 20.1B, C). As a result the epidermis has wide costal zones, clearly differentiated from the intercostal zones (Figure 20.2A, C).

Apart from the microhairs, which are very common (Figure 20.2D), there are no other epidermal appendages present. The microhairs are short with a slightly tapering distal cell (Figure 20.3B, D) which is persistent and not

deciduous as in *P. ecklonii*. The basal and distal cells are about equal in length but the basal cell of the adaxial hairs tends to be longer (Figure 20.3D). Microhair structure, therefore, supports the separation of Group 1E species from those of Group 1D (*P. galpinii* and *P. microphylla*), which also have short awns and rigid, expanded leaves.

The anatomy is clearly of the mesic type although the tissues are generally more dense and compact than is normal for this type. The long cells also have very sinuous walls (Figure 20.2D). These are clearly xerophytic modifications to be expected from a species from arid fynbos communities.

The mesic type anatomy confirms the placement of *P. reflexa* in Group 1 but no further indications are evident from the leaf anatomy. The absence of diagnostic features such as macrohairs and glands make speculation on the possible affinities of this species virtually impossible.

SPECIMENS EXAMINED

CAPE. —3219 (Wuppertal): Cederberg, Algeria, (—AC), Ellis 5578, 5579, 5786.

Group 1F

This group comprises species, with glands either of the raised clavate, sessile elongated or sunken crateriform type (Linder *et al.* 1990). The latter gland type is restricted to taxa in this group. The Group 1F species are mainly from montane grassland communities in the summer rainfall regions of southern Africa, extending northwards into East Africa and Madagascar. They are all typically tufted, caespitose perennials with shortly creeping rhizomes, as are most of the other grasses in these sour grassland communities. Some species (*P. ampla* and *P. glandulosa*) also occur on more fertile soils in the winter rainfall areas.

The anatomy indicates that this is a natural, if variable, grouping. It should be enlarged to accommodate some peripheral species currently placed in neighbouring subgroups, thereby grouping together the summer rainfall glandular *Pentaschistis* species.

P. borussica and *P. natalensis* are undoubtedly closely related and share the sessile elongated gland type with *P. pallida* form G of Group 1B as well as *P. aurea* subsp. *pilosogluma* of Group 2B and a few specimens of *P. setifolia*. *P. natalensis* and *P. pallida* Form G are anatomically very similar whereas *P. borussica*, *P. aurea* subsp. *pilosogluma* and *P. setifolia* share adaxially located sessile elongated glands and compare very closely in overall leaf anatomy. These five taxa can be accommodated in a single subgroup consisting of two closely related nodes with intermediates linking them. Both possess the rare sessile elongated type of multicellular gland, albeit in slightly modified form and location.

P. oreodoxa, *P. setifolia* and *P. glandulosa*, on the other hand, while being closely related to each other, differ from *P. natalensis* and its relatives by possessing either short-stalked clavate or sunken glands. These taxa show

anatomical similarities with *P. galpinii* and *P. microphylla* of Group 1D as well as *P. airoides* subsp. *jugorum* of Group 1C. *P. pallida* form E of Group 1B also undoubtedly belongs with these taxa.

The possible derivation of the unique sunken gland type of *P. setifolia* and *P. glandulosa* is evident in the subglandular cells being sunken in crypts in some instances in these other taxa. Too much emphasis should therefore not be attached to the visually very striking and distinctive sunken crateriform gland type.

P. setifolia serves to link all the taxa of Group 1F in that it sometimes has all these gland types—the short-stalked marginal gland, the sunken crateriform abaxial gland and, very rarely, the sessile elongated adaxial gland. It is truly intermediate in this regard, and if awn development were to be ignored, *P. setifolia* specimens could be assigned to any of the species of Group 1F.

P. ampla, another awnless species, is also difficult to place with any degree of certainty using leaf anatomical criteria but the sunken glands on the inflorescences of some populations support affinities with *P. setifolia* and its relatives. However, other populations are eglandular or with linear glands, suggesting relationships with Group 2 species. This species is also intermediate between the two anatomical groupings accommodated in Group 1F.

Very long, thin microhairs with short distal cells serve to unite all the taxa proposed for this group. These microhairs are considerably shorter in some of the peripheral taxa such as *P. airoides* subsp. *jugorum*, and *P. microphylla* appears to lack abaxial microhairs. Abaxial stomata are also generally lacking in the core taxa but *P. airoides* subsp. *jugorum*, *P. galpinii* and *P. microphylla* have many abaxial stomata. This group is therefore, rather ill-defined and tends to intergrade with allied groups.

21 *P. borussica* (K. Schum.) Pilg. p. 184 (Linder & Ellis 1990a: 55)

A widespread species from the mountains of East and North-east Africa, it is morphologically very variable, with each mountain block having a distinct form, each of which may be recognised as separate subspecies.

No freshly fixed material was available for this anatomical study, consequently reconstituted herbarium material was used. The results, although rather unsatisfactory, are presented here for comparison with the field-collected material of the other species of this group. They, nevertheless, do give an indication of the anatomical structure for comparison with that of the southern African species. The anatomical investigation of this species is, as a result, very superficial, particularly as *P. borussica* displays considerable morphological variation which will undoubtedly also be evident in the leaf anatomy.

The most striking feature of the transectional anatomy of *P. borussica* is the presence of sessile glands on the adaxial ribs and margin of one specimen studied (Figure 21.1A, B). This very unusual gland type and location has

only been rarely observed on *P. aurea* subsp. *pilosogluma* (Figure 40b.1D, F, G) and *P. setifolia* (Figure 24.3H).

The other specimen lacked these adaxial glands but the wide, expanded leaf blade with large, flat-topped adaxial ribs also resembles *P. aurea* subsp. *pilosogluma* closely. The abaxial epidermis has long, thin, flexible macrohairs inserted between a few modified epidermal cells, prickles on the midrib and margin and stomata absent (Figure 21.1D). This epidermal structure is confirmed by Palmer & Tucker (1981) and is very similar indeed to that of the *P. setifolia* specimens without sunken glands (Figure 24.2). The abaxial epidermis of *P. aurea* subsp. *pilosogluma*, as well as *P. natalensis*, although with larger, unthickened hexagonal intercostal long cells, also largely lacks stomata and similar macrohairs may sometimes be present.

An important difference between *P. borussica* and *P. aurea* subsp. *pilosogluma* and *P. natalensis* is evident in the leaf margin. The margin of these other two taxa is typically narrow and tapering (Figures 22.1A, D; 40b.1A, B) whereas *P. borussica* has a truncated margin with a conspicuous sclerenchyma cap (Figure 21.1A, B). This is more similar to the leaf margin of *P. setifolia* and its close allies.

The microhairs of *P. borussica* are also of interest. The basal cell is exceptionally long and finger-like (Figure 21.1D). These microhairs are clearly illustrated in Palmer & Tucker (1981) where they occur on both leaf surfaces. The distal cells are minute, with the basal cells being seven or more times as long. Although the distal cells were not intact in the specimen studied, they presumably are short and tapering as is the case with all the taxa of Group 1F which have elongate finger-like microhairs. This also applies to *P. aurea* subsp. *pilosogluma*.

The anatomical indications are, therefore, somewhat contradictory, but *P. borussica* seems to be more closely related to *P. setifolia* than to *P. aurea* subsp. *pilosogluma* and *P. natalensis*. It undoubtedly belongs in Group 1F.

SPECIMENS EXAMINED

TANZANIA.—Without precise locality, *Rauh* 145; *Goyns* 15.

22 *P. natalensis* Stapf

pp. 184–186 (Linder & Ellis 1990a: 56)

The most widespread species of *Pentaschistis*, ranging from Natal northwards to Tanzania and to Madagascar, *P. natalensis* is a summer rainfall species of montane grassland, usually found on cool, damp mesoclinal south aspect slopes. It often appears to be associated with *Protea* species on quartzitic soils.

P. natalensis has mesic anatomy with diffuse chlorenchyma, intercellular air spaces and small sclerenchyma girders (Figure 22.1). This type of mesic transectional anatomy is normally correlated with the presence of many abaxial stomata but this is not the case with *P. natalensis* where abaxial stomata are very rare or even absent

(Figure 22.2). A similar situation is also found in several of the Group 2B species such as *P. aurea* (Figures 40a.2; 40b.2). It may be significant to note that *P. natalensis* and *P. aurea*, in particular, share the unusual feature of possessing a high frequency of deformed stomata when they are present. *P. pallida* forms D and G, of Group 1B also share this unusual feature of stomata being rare or absent on the abaxial epidermis despite the mesic type anatomy and open, expanded leaf blades.

The small but translucent outer bundle sheath cells are rather conspicuous and, as such, differ from those of most of the preceding species where these cells are smaller and contain chloroplasts and, consequently, are not readily distinguished from the chlorenchyma cells. In this respect these cells closely resemble those of Group 2 species such as *P. pseudopallescens* (Figure 38.1), *P. pallescens* (Figure 39.1) and *P. aurea* (Figures 40a.1; 40b.1). Some Group 1B taxa (*P. pallida* forms D and G) also share this attribute with *P. natalensis*.

A narrow, projecting margin is also characteristic of all the Group 2B species, varying from the very pronounced projection of *P. pallescens* (Figure 39.1) to the situation in *P. aurea* (Figure 40a.1), which is very similar to that exhibited by *P. natalensis* (Figure 22.1A, D). In all cases a definite tapering, pointed margin is present. In *P. pallida* form D this tapering margin is also present (Figure 7d.1).

The adaxial microhairs (Figure 22.3D), in particular, also structurally resemble those of the Group 2B taxa as well as those of Group 1D although they are much thinner than in the latter group. The very short distal cell typifies this microhair type and the adaxial microhairs of *P. pallescens* (Figure 39.3F) and *P. aurea* subsp. *pilosogluma* (Figure 40b.3F, H) are very similar to those of *P. natalensis*. The microhairs of *P. pallida* forms D and G are not of this type with the basal and distal cells being almost equal in length. Robbertse (1959) also illustrates this type of microhair for *P. natalensis*.

Although foliar glands do not occur on the southern populations of *P. natalensis*, *Simon* 2327 from Zimbabwe does have glands on its leaves. These glands are identical to those illustrated for *P. aurea* subsp. *pilosogluma* (Figures 40b.1G; 40b.2F; 40b.3D) and which also occur on *P. borussica* (Figure 21.1A, B) and sometimes *P. setifolia* (Figure 24.3H) i.e. the sessile elongated type adaxially located on the ribs. This gland type also occurs on the keels of the glumes of *P. natalensis*, *P. pallida* form G and *P. cirrhulosa* (Linder *et al.* 1990). These glands are oval to elongated in surface view, lack ring cells and the gland surface is convex to flat. This type of gland is also present on the leaf margins of *P. pallida* Form G (Figures 7g.1; 7g.2A, B; 7g.3E, F).

The overall anatomical evidence suggests close ties for *P. natalensis* with the species of Group 2B, all of which have the linear gland type. The implications of these character distributions are that the sessile elongated gland type and the linear type are actually not distinct but represent different extremes of a continuum. The linear glands are narrower, longer, and less well differentiated than the sessile, elongated gland type but both lack collar

cells. The latter can easily be derived from the former as suggested by Linder *et al.* (1990) and this is corroborated by the leaf anatomy and the taxonomic distribution of taxa with these gland types.

The inclusion of *P. natalensis*, *P. borussica*, *P. ampla* and *P. pallida* forms D and G in a separate group (close to Group 2B) will result in a more natural grouping of those taxa possessing the same gland types, delineating two groups each with a basically different gland type.

In addition, the sunken gland type, which is unique to some species of this Group 1F (*P. setifolia* and *P. glandulosa*), can also be derived from this sessile elongated gland as shown by the subglandular tissue sunken in crypts in *P. galpinii* (Figure 17.1E). This serves to emphasize that *P. oreodoxa*, *P. setifolia* and *P. glandulosa* cannot be excluded from this alliance. They also share similar microhairs and macrohairs and lack abaxial stomata but do not have tapering leaf margins or translucent outer bundle sheath cells. The presence of short-stalked glands in some specimens of *P. setifolia* and *P. oreodoxa*, however, indicate that they cannot be accommodated in a group excluding clavate glands.

SPECIMENS EXAMINED

TRANSVAAL.—2430 (Pilgrims Rest): Mount Sheba, (—DC), Ellis 4461. 2530 (Lydenburg): Mount Anderson, Long Tom Pass, (—CA), Ellis 5735, 5736, 5737. 2531 (Komatipoort): Barberton, (—CA), Ellis 1542.

NATAL.—3029 (Kokstad): Franklin, (—AD), Ellis 225.

23 *P. oreodoxa* Schweick.

pp. 187–190 (Linder & Ellis 1990a: 57)

A Drakensberg endemic occurring in alpine and sub-alpine grasslands over a wide altitudinal range, it often occurs with *P. setifolia*, a species which it resembles morphologically and ecologically. It is not certain whether these two species are separated correctly, the only apparent difference being in the degree of development of the lemma awns. This questionable relationship between the two taxa is confirmed by the leaf anatomy which is virtually identical in all respects except for the presence of sunken crateriform glands in some populations of *P. setifolia*. This gland type does not occur in *P. oreodoxa*.

The leaf anatomy of *P. oreodoxa* and that of *P. setifolia* and *P. glandulosa* is very similar indeed with a gradation through these three taxa. No clear anatomical disjunctions separate these species. Slightly raised marginal glands sometimes occur on *P. oreodoxa* (Figures 23.2E, F; 23.3D, H) but most specimens are without foliar glands. *P. setifolia* is also often without glands (Figure 24.1) but raised marginal glands are sometimes present (Figures 24.3F, G; 24.4C, H). The specimens of *P. setifolia* share very similar anatomical attributes with *P. oreodoxa*. However, a large proportion of the sample of *P. setifolia* specimens has sunken crateriform glands (Figures 24.3A–F; 24.4A–F; 24.5) which do not occur on *P. oreodoxa* but are very common on *P. glandulosa* (Figures 26.1–26.3). This is not consistently so and specimens of both *P. setifolia* and *P. glandulosa* without sunken glands

do occur and these cannot be separated from *P. oreodoxa* using anatomical criteria.

Other characters such as microhair structure, the type of macrohairs, the presence of costal prickles, the absence of abaxial stomata and similar transectional anatomy serve to unite these into a very closely related group. All these features in combination are diagnostic for these three species (although they are not all always present on all specimens) and serve to separate them from all other *Pentaschistis* taxa.

In transectional anatomy, *P. pallida* form C (Figure 7c.1) can be confused with this group, as the leaf outline and structure is similar. However, the epidermal cellular pattern is different, indicating that the transectional similarity is only superficial. Stomata may be present on *P. pallida* form C (Figure 7c.2), and the macrohairs, when present, are radically different (Figure 7c.3C, F) from those of *P. oreodoxa*. The anatomy indicates, however, that *P. pallida* form E (Figure 7e.1) does belong with *P. oreodoxa* and its allies. This applies to all anatomical characters except that *P. pallida* form E does not possess sunken glands, as does *P. oreodoxa*.

SPECIMENS EXAMINED

NATAL.—2828 (Bethlehem): Mont-aux-Sources, Sentinel Peak, (—DB), Ellis 3132*, 3143, 3146*, 3151*, 5729, 5731*, Du Toit 645, 647*, 664, 665, 666, 2829 (Harrismith): Cathedral Peak, summit of Organ Pipes Pass, (—CC), Ellis 1403*, 1407*; Organ Pipes Pass, (—AA), Ellis 5718, 5721, 5722, 2929 (Underberg): Sani Pass, (—CB), Du Toit 2205*, 2281, 2282*, 2290, 2291*, 2305, Ellis 5706*, 5707; Thamatuwe Pass, (—CC), Killick & Vahrmeijer 3992.

* specimens with leaf glands.

24 *P. setifolia* (Thunb.) McClean

pp. 191–197 (Linder & Ellis 1990a: 58)

A widespread summer rainfall species extending northwards from the Grahamstown District as far as Harrismith, it always grows in mountain grassland and can be a dominant species in these communities. It is a typically caespitose species, usually awnless but the lemma awn may be relictual. It often occurs with *P. oreodoxa* or, in the south, *P. glandulosa*, both of which are awned.

This species is very variable morphologically, particularly in the occurrence of the sunken leaf glands, the shape of the inflorescence and in the growth form and shape of the plants. In the Natal Drakensberg, where it occurs with *P. oreodoxa*, no leaf glands are present, the inflorescences are compact and occasionally one lemma is awned. In all these respects it approaches *P. oreodoxa* morphologically. In the eastern Cape, *P. setifolia* often approaches *P. glandulosa*, especially in the possession of leaf glands. This geographical variation pattern is also evident in the leaf anatomy and *P. setifolia* is intermediate between *P. oreodoxa* and *P. glandulosa* in character state distribution.

Gland type and presence is variable. Leaf glands may be absent (Figures 24.1; 24.2), or present as sunken glands (Figures 24.3A–F; 24.4A–F), or slightly raised oval glands

on the margin (Figures 24.3G, H; 24.4H) or both gland types may occur (Figure 24.4C). Similarly the other epidermal appendages are also variable in their occurrence with microhairs, macrohairs and prickly hairs being either present or absent. The macrohairs, when present, are typical of those found on *P. oreodoxa* and *P. glandulosa* in that they are inserted into a base consisting of one or two inflated epidermal cells. In all respects the leaf anatomy of *P. setifolia* resembles that of these other two species very closely indeed and they cannot be separated on the basis of leaf anatomy.

SPECIMENS EXAMINED

O.F.S. — 2827 (Senekal): Cloccolan, (—DC), *Ellis & Loxton* 985, 2828 (Bethlehem): Golden Gate Highlands National Park, Brandwag Kop, (—DA), *Ellis* 2374, 2377, 2378, Wodehouse Peak, *Ellis* 2380+, 2388+, 2389+.

NATAL. — 2829 (Harrismith): Cathedral Peak, summit of Organ Pipes Pass, (—AA), *Ellis* 5719+; lookout on Organ Pipes Pass, (—CC), *Ellis* 3301+.

CAPE. — 3028 (Matatiele): Qacha's Nek Pass, (—BA), *Ellis* 5697*; Naudesnek Pass, (—CA), *Ellis* 5684+, 5692*+, 5693*+. 3126 (Queenstown): Jamestown, (—BB), *Ellis* 2601; Penhoek Pass, (—BC), *Ellis* 2595, 2596. 3227 (Stutterheim): Cathcart, (—AC), *Ellis* 2611*, 2612*+, 2613*+, 2614*; Dohne, (—AD), *Ellis* 308; Old Thomas River, (—CA), *Ellis* 5818*.

* specimens with sunken glands.

+ specimens with sessile but raised glands.

25 *P. ampla* (Nees) McLean

pp. 197, 198 (Linder & Ellis 1990a: 59)

This is a summer-flowering species from the lower reaches of the mountains of the southern and western Cape Province from Port Elizabeth to Clanwilliam, and is very poorly represented by two specimens which were collected and fixed in the field. The sampling intensity is inadequate to gain a firm understanding of the leaf blade anatomy and it is impossible to draw any conclusions regarding relationships of this interesting species.

The insufficient material of *P. ampla* studied is particularly unfortunate as this species appears to be somewhat intermediate between the two groups of taxa included in Group 1F. The specimen illustrated in Figure 25.1 differs considerably from the others examined from herbarium specimens. In these, the long cells are longer, narrower and fusiform in shape with numerous microhairs present. Stomata are absent on all specimens except one (*Taylor* 4575), where they are irregular in occurrence and shape. Several deformed stomata were observed, a condition similar to that observed in *P. natalensis* and *P. aurea*. These specimens also have thinner leaves with tapering margins and the parenchyma sheath cells are without chloroplasts. This anatomy is very similar to that of *P. natalensis*, a species which also resembles *P. ampla* morphologically, particularly their growth forms where the culms arise from flat, woody discs.

The specimen illustrated (Figure 25.1) differs considerably from *P. natalensis* in leaf anatomy. The leaf is thicker, with deep adaxial furrows, a thick cuticle is present and the margin is abrupt. The intercostal long cells are also much shorter and wider.

These anatomical differences may be correlated with the morphological differences of the two forms within *P. ampla*: eastwards from the Cape Peninsula specimens have scattered glands on the inflorescence, whereas material from west and north of the Peninsula is usually eglandular. Geographically these anatomical vouchers agree with this distribution and the differences between *Ellis* 5591 (illustrated in Figure 25.1) from the Cederberg and the remainder of the sample may possibly be explained on this basis. It is also possible that the voucher specimens were incorrectly identified, as *P. ampla* and *P. aurea* are difficult to separate, especially if the characters of the base are not evident. Additional material is required before an adequate understanding of the anatomical character patterns in this species can be gained.

SPECIMENS EXAMINED

CAPE. — 3219 (Wuppertal): Cederberg, Algeria, (—AC), *Ellis* 5591. 3318 (Cape Town): Kenilworth Race Course, (—CD), *Linder* 4864; Stellenbosch, (—DD), *Taylor* 4575. 3319 (Worcester): Du Toitskloof, Fisantekraal, (—CA), *Esterhuysen* 28112.

26 *P. glandulosa* (Schrader) Linder

pp. 199–202 (Linder & Ellis 1990a: 60)

This species occurs in the fertile soils in the winter rainfall area, which extends from Vanrhynsdorp southwards to the Peninsula and eastwards to Humansdorp, and then northwards as far as Stutterheim in summer rainfall grassland. It is a strongly caespitose plant, often with sunken glands. It can be distinguished from *P. setifolia* by its awned lemmas but is very difficult to separate from *P. oreodoxa*, particularly in the southern Drakensberg.

These three species are very variable in the presence of the diagnostic sunken leaf glands. In some populations this gland type is consistently present and common, whereas in others they are rare or even absent. There appears to be no geographical relationship involved here as indicated by the provenances of the specimens studied. In general, sunken glands are most common in the Border populations, extending only as far northwards as Qachas Nek. However, populations in close proximity may exhibit either state. An example is *P. glandulosa* from the Suurburg, where plants from the Suurburg National Park are without glands, but those from further inland are very glandular.

The relationships of *P. glandulosa* undoubtedly lie with *P. setifolia* and *P. oreodoxa* as well as *P. pallida* form E. These species share the same type of microhair and macrohair. Abaxial stomata are absent and there is a trend toward the development of a continuous abaxial hypodermal sclerenchyma layer. This is further discussed under these two species.

SPECIMENS EXAMINED

CAPE. — 3124 (Hanover): Compasberg, (—DC), *Linder* 5070. 3227 (Stutterheim): Stutterheim, Old Thomas River, (—AC), *Ellis* 5815*, 5817*; 17 km NW of Stutterheim, (—AD), *Ellis* 2610*. 3321 (Ladismith): Groot

* specimens with sunken glands.

Swartberg, Gamkaskloof area, (–BD), *Ellis* 5630*, 5631*. 3323 (Willowmore): Uniondale Poort, (–CA), *Ellis* 5828; Avontuur, *Ellis* 5829. 3324 (Steytlerville): Groot Winterhoek Mts, Cockscomb Peak, (–DB), *Ellis* 5609. 3325 (Port Elizabeth): Suurberg National Park, (–BC), *Ellis* 5833, 5834; Suurberg Pass, *Ellis* 5836*, 5838*, 5839*, 5840*; Groendal Dam, 23 km W of Uitenhage, (–CB), *Ellis* 2569. 3419 (Caledon): Rivier-sonderend Mts, Die Galg, (–BA), *Ellis* 5808*, 3421 (Riversdal): Albertina, (–BA), *Ellis* 1653; 23 km W of Mossel Bay, (–BB), *Ellis* 629*.

* specimens with sunken glands.

Group 1G

This group of species is restricted to the tropical African mountains and no representatives occur in southern Africa. Plants assigned to this group sometimes have stalked glands and the inflorescence is contracted and even spike-like. The classification of this group of species has not been clarified and many problems remain to be resolved. Populations from different mountain blocks differ slightly and cannot be recognised as separate species as they overlap morphologically. The correlation between the geographical distribution patterns and the morphological variation exhibited is ill-defined and detailed analyses are required before changes to the taxonomy can be justified.

No freshly fixed material of any species from this species group was available for anatomical study. Consequently herbarium specimens had to be used, often with unsatisfactory results due to poor rehydration and hand sectioning. The interpretation of the anatomical structure is hampered by these poor preparations and they generally do not photograph well. The few results obtained are presented here but caution must be exercised in their interpretation. It is known that most of these Group 1G taxa exhibit excessive morphological variation and the very inadequate anatomical samples may be misleading and not fully representative of the anatomy of their species. No inferences on possible relationships can be made due to these inadequacies in the basic study material.

P. minor and *P. mannii* were the only species of Group 1G which were studied. *P. imatongensis*, *P. pictigluma* and *P. gracilis* were not studied anatomically and are not discussed in this paper.

27 *P. minor* (Ballard & C.E. Hubb.) Ballard & C.E. Hubb. p. 203 (Linder & Ellis 1990a: 62)

This species is widespread on the higher mountains of East Africa. It ranges as high as the alpine zone. Only two specimens were examined and it is unclear how representative these are of habitat extremes and geographical variation patterns.

The leaf blades of *P. minor* are typically of the mesic type but are noteworthy in being exceptionally thin (Figure 27.1A) and display no xerophilic features, which is unusual in an alpine species. They are inrolled, with well-developed adaxial ribs and furrows, with 3 or 5 first order bundles separated by 1 or 2 smaller bundles. No glands

were observed and the abaxial epidermis is covered by a continuous cuticle and has no stomata.

The abaxial epidermis shows clear zonation. The intercostal long cells are elongate, rectangular with sinuous walls and are separated by a single tall intercostal silica body (Figure 27.1B). Stomata, prickles and macrohairs do not occur but the microhairs are noteworthy in being very elongate with a tapering distal cell. The silica bodies are irregularly dumbbell-shaped.

SPECIMENS EXAMINED

Schlieben 4844; *Arambourg* 188.

28 *P. mannii* Stapf ex C.E. Hubb. p. 203 (Linder & Ellis 1990a: 62)

A species with stalked pedicel glands and with narrow, infolded leaves, it is endemic to Mt Cameroun in West Africa in montane grassland between 3 000 and 4 000 m.

The leaf anatomy shows clear xeromorphic adaptations in that the abaxial sclerenchyma girders are well developed, sometimes forming distinct 'knees', the leaf blades are narrow and infolded and abaxial stomata appear to be absent (Figure 28.1). In one specimen examined, the blades are unusual in the total absence of adaxial sclerenchyma strands or girders (Figure 28.1B).

No epidermal scrapes were successful and the epidermal structure was not examined. Nevertheless, the anatomy is clearly of the mesic type, although exhibiting considerable modification from the classic type, and this species clearly belongs with the glandular species of Group 1.

SPECIMENS EXAMINED

Koechlin 7608; *Meurillon* 1198.

Group 2

This group is distinguished by the possession of sessile linear glands in contrast to the stalked, multicellular glands of Group 1 species (Linder & Ellis 1990a) and the eglandular condition in all other groups. These glands are not always present on the leaf blades but may be restricted to the pedicels and inflorescence rachis and branches.

The linear glands are usually only visible with transmitted light and not with the SEM, as they are flush with the epidermis and their cell outlines are not differentiated in surface view. These glands are usually uniseriate in files up to 25 cells long with the terminal cells narrower and tapering. The gland cells are about 1.5 times larger than the costal epidermal cells as seen in transverse section. In the leaf margins these linear glands may be up to nine cells wide. This gland type is fully described and discussed in Linder *et al.* (1990).

Group 2 is heterogeneous for the two basic leaf types found in the southern African arundinoid grasses. These two anatomical subdivisions are defined and discussed fully in the introduction. Thus the mesic type occurs in all representatives of Group 2B, whereas Group 2A has the sclerophyllous type, albeit somewhat modified from the typical condition.

Apart from the shared possession of the sessile linear type of gland, the two subdivisions of Group 2 do not share similar leaf anatomy and do not appear to be closely related. In *Pentaschistis* the possession of multicellular glands is strongly correlated with the mesic/sclerophyllous dichotomy and very few taxa with sclerophyllous leaf anatomy possess glands. The only exceptions are the species of Group 2A (where the glands are not often present on the leaf blades) and *P. lima* and *P. cirrhulosa* of Group 1B. These latter two species also do not have foliar glands but they do have permanently infolded leaf blades resembling the sclerophyllous type. However, the mesophyll is not of the compact type with small isodiametric cells that is characteristic of the sclerophyllous type, indicating that this structure may actually represent highly modified mesic anatomy. The true affinities of all these anomalous taxa are not clear yet, but it appears significant that they all differ in some respects from the typical sclerophyllous type. This may signify that their sclerophyllous-like anatomy is actually a modification of the mesic type. If this is indeed so, then the correlation between mesic anatomy and the possession of glands will still hold and the subgeneric separation of the glandular (Groups 1 and 2) and the eglandular (Groups 3–6) *Pentaschistis* taxa will be supported by this additional fundamental feature of the leaf anatomy.

Group 2 also differs from Group 1 in the absence of dumbbell-shaped silica bodies, particularly in Group 2A. This type of silica body also appears to be correlated with the mesic type of leaf anatomy and it is not surprising, therefore, that those representatives belonging to Group 2A that have the sclerophyllous type of leaf anatomy, also do not have dumbbell-shaped silica bodies. In the more mesic members of Group 2B, irregular dumbbell-shaped silica bodies occur.

In contrast to Group 1, where individual species are generally not recognizable on anatomical criteria, Group 2 species are often clearly separable on leaf anatomy, each species usually possessing unique diagnostic features. Clear anatomical disjunctions are present between species and they do not intergrade as so often is the case with Group 1 taxa where clinal variation patterns are of general occurrence. Small anatomical samples are often sufficient to describe the anatomy of a given species and additional replications tend to contribute very little additional information. This applies particularly to Group 2A (and Groups 3–6) but in Group 2B there are similar tendencies to those observed in Group 1 with the complex variation patterns being difficult to interpret.

Group 2A

The taxa of Group 2A seem to be isolated from the rest of the genus on the basis of their leaf anatomy. Their

swollen, villous tiller bases also serve to separate them from other *Pentaschistis* taxa. Although they share sessile linear glands with Group 2B taxa, there is little else to indicate that this reflects a close phylogenetic relationship. The basic anatomical type of Groups 2A and 2B also differs with group 2A being of the sclerophyllous type and Group 2B of the mesic type.

As shown by Linder *et al.* (1990), the sessile linear gland type is not consistently present on all specimens of Group 2A and plants may be eglandular. When present they are usually restricted to the pedicels and are difficult to detect except in transverse sections. Studies of the leaf anatomy consequently contribute little to our knowledge of gland occurrence and morphology in this group. However, further study of the glands in this group is essential in order to ascertain whether the correlation between possession of glands and the mesic type of leaf anatomy really does break down in this group.

Although all taxa in this group are geophytes with swollen underground bases, the anatomy indicates that it does not constitute a monophyletic entity and the constituent species separate into two distinct groups—*P. aristidoides* and *P. veluina* being distinct from *P. viscidula* and *P. argentea*. The latter two species show anatomical and morphological similarities with some species of *Merxmüllera*, such as *M. lupulina* and *M. rufa*. However, glands are unknown in *Merxmüllera* and the spikelet morphology of *P. argentea* and *P. viscidula* agrees well with that of *Pentaschistis* as they only have two florets. The taxonomic position of this group needs further detailed investigation which should include the species of *Merxmüllera* mentioned above. This study should also shed light on the natural delimitation of *Pentaschistis* and *Merxmüllera*, two genera which appear to be artificially circumscribed as currently defined.

32 *P. aristidoides* (Thunb.) Stapf

pp. 204–208 (Linder & Ellis 1990a: 65)

Morphologically this is a very homogeneous species but the leaf anatomy is exceptionally variable. The variation is unusual due to the magnitude of the structural differences and that it is not characterized by patterns or trends. In addition the indications from transectional and epidermal anatomy do not correspond.

Anatomical characters which vary are: adaxial surface with slight to massive ribs with shallow to cleft-like furrows (Figure 32.2A–D), abaxial girders absent, as small strands, trapezoidal girders or fused, forming a continuous subepidermal layer (Figures 32.1B, E; 32.2A–D; 32.3B, E, G), chlorenchyma diffuse with large intercellular air spaces (Figures 32.2C, D; 32.3B, E, G) or more compact with larger angular cells (Figures 32.1B, E; 32.2A), epidermal zonation undifferentiated (Figures 32.1C, F; 32.3C) or differentiated (Figure 32.3F, H, J), stomata absent (Figures 32.1C, F; 32.3C, F) or present (Figures 32.3H, J; 32.4C), abaxial microhairs present (Figures 32.1C, F; 32.4A) or absent, macrohairs usually absent but soft, superficial hairs rarely present (Figures 32.3F; 32.4E).

The lack of congruence between the leaf transverse sections and the abaxial epidermal scrapes is unusual. An example is where the abaxial sclerenchyma girders are fused to form a continuous hypodermal layer as in Figure 32.1. This condition is normally associated with an epidermal pattern where costal and intercostal zones are not differentiated and where stomata are absent as in Figures 32.1C, F. The absence of stomata is confirmed in the transections where none are visible in the abaxial epidermis (Figure 32.1B, E). In other specimens, however, this is not the case. Figure 32.3B illustrates a leaf where stomata are clearly visible in section (arrowed) but they are absent from the epidermal preparation (Figure 32.3C) which also does not exhibit zonation. This suggests a subepidermal sclerenchyma layer but it is not present (Figure 32.3B). The opposite condition may also occur, as in Figure 32.3J which is the epidermis of Figure 32.2A. Here stomata are present on the epidermal scrape but not evident in the transverse section.

A possible explanation for this is that the material examined was not always comparable, as it appears from the voucher specimens, that both the broad flag leaves from the base of the flowering culms and the narrower basal leaves from new vegetative tillers were sampled, sometimes even on the same plant. These different leaves probably differ considerably in their leaf anatomy (Metcalf 1960) and this may contribute to the confusing results of this study.

Despite this anatomical variation, certain taxonomic deductions can be made. The anatomy of *P. aristidoides* is intermediate between the mesic and sclerophyllous fynbos grass leaf types as described in the introduction, particularly with respect to the nature of the mesophyll tissue which is not compact or composed of small, isodiametric cells. This mesophyll type is clearly illustrated by Robbertse (1959) for *P. aristidoides*. This feature is shared with *P. velutina* but not *P. viscidula* or *P. argentea*, also of Group 2A. The latter two species have typical sclerophyllous transectional anatomy with compact, small isodiametric cells, but they have abaxial stomata. Several specimens of *P. aristidoides* also have abaxial stomata (Figures 32.3H, J; 32.4C) but these are not necessarily associated with specimens with compact chlorenchyma. However, Ellis 5566 (Figures 32.3I, J; 32.2A) strongly resembles this type.

P. aristidoides and *P. velutina*, therefore, show close anatomical links, closer than either species shows with *P. argentea* and *P. viscidula*. The differences between them seem to be of a fundamental nature, involving the structure of the mesophyll, and may be taxonomically meaningful.

The abaxial microhairs of *P. aristidoides*, which are only rarely present, closely resemble those of *P. argentea* in being short and wide with the basal cell equal to or shorter than the distal cell (Figures 32.4A; 35.3B). This type of microhair does not occur on any of the other glandular species of Groups 1 and 2 but is sometimes found on representatives of the eglandular species of Groups 3A [*P. colorata* (Figure 41.5B, F) and *P. malouinensis* (Figure 48.3B)] and 3B [*P. exserta* (Figure 54.3B, C)] as well as on *Merxmuellera stricta* (Ellis 1980b).

Microhair structure is generally considered to be useful taxonomically and the distribution of this rare type of microhair in *Pentaschistis* and its allies may indicate phylogenetic affinities.

The adaxial microhairs of *P. aristidoides* differ substantially from those on the abaxial surface. They are elongate with rather small distal cells (Figure 32.4B, D, F) as illustrated by Robbertse (1959) as well. This hair type tends towards the type present in *P. velutina* (Figure 33.3D, F) and which is characteristic of most of the taxa of Group 4 as well as *Pentameris*. These distinctive adaxial microhairs of all these latter taxa are extremely narrow and elongate with a minute distal cell. The hairs of *P. aristidoides* cannot be grouped with them but undoubtedly tend toward them and resemble those of some Group 2b species most closely e.g. *P. pallescens* (Figure 39.3E, F). The adaxial microhairs of *P. aristidoides* also differ considerably from those of all the taxa which share the same short abaxial microhairs mentioned above. The evidence from the microhairs is, consequently, inconclusive and confusing.

The anatomy indicates, therefore, that *P. aristidoides* is a truly intermediate species showing links with several other supraspecific groupings in *Pentaschistis* and even neighbouring genera such as *Pentameris* and *Merxmuellera* as represented by *M. stricta* (abaxial microhairs), *M. rufa* and *M. lupulina* (sclerophyllous transectional anatomy with abaxial stomata). Unfortunately the evidence is compromised due to the excessive degree of variation observed, which may be further compounded by the sampling of non-comparable leaves. Further attention must be given to the leaf anatomy of *P. aristidoides* as it appears to be central to our understanding of the relationships of several of the groupings in *Pentaschistis* and may even be indicative of a hybrid origin.

SPECIMENS EXAMINED

CAPE.—3118 (Vanrhynsdorp): Gifberg, (—DC), Ellis 5778. 3218 (Clanwilliam): Olifants River Mts, (—BD), Ellis 5428. Uitkomsberg, Ellis 5785. 3219 (Wuppertal): Cederberg, Algeria, (—AC), Ellis 2504, 5787; Kouebokkeveld Mts, (—CA), Ellis 2487. 3319 (Worcester): Du Toitskloof Pass, (—CA), Ellis 2857; Franschoek Pass, (—CC), Ellis 2349. 3418 (Cape Town): Peninsula. Helderberg Nature Reserve, (—AB), Ellis 2355, Scarborough, Ellis 5440; Gordon's Bay, (—BB), Ellis 676, Sir Lowry's Pass, Ellis 2282, 2283. 3419 (Caledon): Riviersonderend Mts, (—BA), Ellis 5566, 5806; Viljoenshof, (—CA), Ellis 5992.

33 *P. velutina* Linder

pp. 209–211 (Linder & Ellis 1990a: 66)

This species is rare with distinct anatomy. The thick but narrow leaf, with tapering margins and massive ribs is characteristic of this species, this distinctive outline being diagnostic (Figure 33.1A, C). The leaf outline alone, serves to distinguish *P. velutina* from all other species of *Pentaschistis*.

The anatomy is of the sclerophyllous type except that the chlorenchyma is rather diffuse with many intercellular air spaces (Figure 33.1B, D). This unusual feature is shared with some specimens of *P. aristidoides* (Figure 32.2) but not with the other species of Group 2A—

P. viscidula and *P. argentea*. An undescribed segregate of *P. viscidula* also has this type of chlorenchyma (Figure 34.4A, B) and may actually belong with or close to *P. velutina*. This chlorenchyma configuration, although superficially resembling the sclerophyllous type, may only reflect an extreme modification of the mesic type and therefore, indicates affinities with the glandular *Pentastichis* species of Groups 1 and 2.

The abaxial epidermis is unique in Group 2A in possessing short (2–7 cells), uniseriate files of gland-like cells which may be homologous with sessile linear glands (Figure 33.2). This type of gland is diagnostic of Group 2, but is restricted to the pedicels of the other species of Group 2A. In Group 2B these linear glands occur on both leaves and pedicels but consist of more than seven cells per gland and taper gradually at either end.

Abaxial stomata and microhairs are absent, which is not the case in *P. viscidula*, *P. argentea* and in many specimens of *P. aristidoides*. The adaxial microhairs of *P. velutina* also differ from those of the other Group 2A species. They are very elongated and narrow with a minute distal cell (Figure 33.3D, F), resembling those of the Group 4 *Pentastichis* species as well as *Pentameris*. These hairs on *P. aristidoides* tend towards this elongate type (Figure 32.4B, D, F).

Specimens which are intermediate between *P. velutina* and *P. curvifolia* are known from the Porterville Mountains, suggesting a hybrid origin. It may be relevant to note that the adaxial microhairs of both these species are identical, as reference to Figure 57.3C & F clearly shows. This appears to support a link with the species of Group 4 even though *P. velutina* is glandular.

The affinities of *P. velutina* are also obviously close to *P. aristidoides*, but the leaf anatomy does not support close links with *P. viscidula* and *P. argentea*. Anatomically and morphologically this is a distinct species, intergrading with no other species.

SPECIMENS EXAMINED

CAPE.—3219 (Wuppertal): Cederberg, Pakhuis Pass, (–AA), *Ellis* 4630; Cederberg, Sneekop, (–AC), *Ellis* 5512; 16km from Citrusdal on road to Ceres, (–CA), *Ellis* 2490; Porterville Mts, (–CC), *Ellis* 5798, 5799.

34 *P. viscidula* (Nees) Stapf

pp. 212–215 (Linder & Ellis 1990a: 68)

This species has unmistakable anatomy, being characterized by the well-developed abaxial ribs and furrows (Figure 34.1) along which lie macrohairs which are unusual in being unicellular, stiff and pointed with a constricted and superficial base associated with only a few specialized, raised epidermal cells (Figures 34.2; 34.3). These hairs are readily deciduous due to this superficial insertion in the epidermis and, consequently are often not present on specimens.

Both these characters are unique in *Pentastichis* although abaxial furrows do occur in some other arundi-

noid taxa such as *Dregeochloa* (Ellis 1977), *Merxmuellera dura* (Ellis 1982) and *M. decora* (Ellis 1983), *Centropodia glauca* (Ellis 1984) and *Chaetobromus involucratulus* (Ellis 1988). In most of these species the abaxial furrows are narrow and cleft-like and the leaf section is not moniliform as in *P. viscidula*. The unusual abaxial macrohairs are virtually identical to those of *Chaetobromus involucratulus* (Ellis 1988) in both location and form. As there are no other indications that *Chaetobromus* and *P. viscidula* are closely related, it appears as if this unusual hair type has evolved independently in each of these taxa. Neither of these diagnostic characters of *P. viscidula*, therefore, appears to elucidate phylogenetic relationships.

Morphologically *P. viscidula* and *P. argentea* are undoubtedly closely related. The basic anatomical structure of these two species is also very similar but closely resembles that of *Merxmuellera lupulina* and *M. rufa* (Ellis 1983). This similarity will be discussed further under *P. argentea*.

Ellis 5589 (Figure 34.4) differs greatly in leaf anatomy from other specimens of *P. viscidula*, and appears to represent a new, undescribed species nearer *P. velutina* as discussed under that species. Although this specimen does have macrohairs, these are very different from those of *P. viscidula*, being soft and flexible with cushion cells at the base. These macrohairs and the abaxial epidermis in general are very similar to those observed on *Ellis* 5498 which, although sterile, has been tentatively placed near *P. aristidoides*. This specimen does not have a narrow leaf blade but the lateral parts of the lamina are thicker than the central parts (as in *Ellis* 5589) and it closely resembles *P. aristidoides* in transectional anatomy. This is confirmed by the ultrastructure which shows microhairs similar to those of *P. aristidoides*. The plants grow together with *P. aristidoides* and *P. viscidula* but flower at least a month later than either of these two species. The anatomy demonstrates that these specimens (*Ellis* 5498, 5589) should be placed close to *P. aristidoides* and *P. velutina* rather than here in *P. viscidula*. An assessment of the morphology of this taxon awaits the collection of adequate flowering material.

SPECIMENS EXAMINED

CAPE.—3219 (Wuppertal): Cederberg, Algeria, (–AC), *Ellis* 5589 (= new species); Groot Winterhoek Mts, Suurvlak Farm, (–CC), *Ellis* 5488, 5489, 3319 (Worcester); Groot Winterhoek Mts, Groenberg, (–AA), *Ellis* 5491, 5492, 5498 (= new species); Hex River Mts, Milner Peak, (–AD), *Ellis* 5529, 3419 (Caledon); Riviersonderend Mts, Wa-en-Osse Peak, (–BA), *Ellis* 5558.

35 *P. argentea* Stapf

pp. 216–219 (Linder & Ellis 1990a: 68)

The transectional leaf anatomy of *P. argentea* and *P. viscidula* is typical of the sclerophyllous type with compact mesophyll of small isodiametric cells with minute intercellular air spaces. Sclerenchyma is abundant with well-developed girders present, but none of this supporting tissue is lignified. This sclerophyllous anatomy is also illustrated by Robbertse (1959) showing clearly the compact chlorenchyma of angular cells without air spaces.

Although very similar in basic anatomical structure, *P. argentea* and *P. viscidula* can readily be distinguished by the leaf outline. Abaxial ribs and macrohairs are absent on *P. argentea*. In all other respects these two species share very similar anatomy.

In all other *Pentaschistis* species with this type of cross-sectional anatomy (e.g. the species of Groups 3 and 4) the abaxial epidermis is characterized by the absence of stomata and zonation is usually not evident as well. This is not the case with *P. argentea* and *P. viscidula* where abaxial stomata are numerous in clearly distinct intercostal zones (Figures 34.2; 35.2). These low dome-shaped stomata are separated by single interstomatal cells in stomatal files and these files adjoin one another. The abaxial stomatal density of these leaves is, therefore, relatively high—even greater than that of many species with mesic type leaves as in Group 1. In transverse section these intercostal stomata are visible (Figure 35.1B, D, F, H) flush with the abaxial epidermis. Of interest are the very small substomatal chambers beneath these stomata.

This type of sclerophyllous anatomy is also found in *Merxmuellera lupulina* and *M. rufa*, with *M. decora* tending to this anatomical type (Ellis 1983). These three species differ only in leaf outline from *P. argentea* and *P. viscidula*, with each species exhibiting a characteristic transectional outline. As all the species concerned are geophytes (Linder & Ellis 1990b), and share similar growth forms and habitats, it is not clear whether these anatomical resemblances are the result of convergent evolution or a common phylogenetic history.

There are major spikelet differences between these two *Pentaschistis* species and the anatomically similar *Merxmuellera* species (2 vs 3–10 florets). Glands are also unknown in *Merxmuellera*. Before the phylogenetic implications of the anatomical resemblances between them can be appreciated, the correct circumscription of both these genera must be established by a synthesis of all characters. Leaf anatomy alone cannot provide sufficient evidence for their taxonomic realignment. However, it must be noted that *M. rufa* and *M. lupulina* are distinct in the genus and differ in leaf anatomy from all other *Merxmuellera* species (Ellis 1983) and resemble *P. viscidula* and *P. argentea* very closely indeed. This resemblance is much closer than that which these two species exhibit with the other species of Group 2A—*P. aristidoides* and *P. velutina*.

The microhairs of *P. argentea* are of interest. Abaxial hairs are short with distal and basal cell of equal length (Figure 35.3B) (Robbertse 1959) and adaxial microhairs appear to be absent. In *P. viscidula*, on the other hand, adaxial microhairs do occur and these, as well as the abaxial hairs, have a distal cell much shorter than the basal cell. They are also much more finger-like than the microhairs of *P. argentea*.

SPECIMENS EXAMINED

CAPE.—3319 (Worcester): Groot Winterhoek Mts, Groenberg, (—AA), Ellis 5493, 5494. 3320 (Montagu): Langeberge, Tradou Pass, (—DC), Ellis 658, 5154, 5541; Grootvadersbos, (—DD), Ellis 5552, 3321 (Ladismith): Langeberge, Garcia's Pass, (—CC), Ellis 2542, 3322

(Oudtshoorn): Outeniqua Mts, Robinson Pass, (—CC), Ellis 2554, 3418 (Cape Town): Hottentots Holland Mts, Sir Lowry's Pass, (—BB), Ellis 2284, 2285, 2290, 2291. 3419 (Caledon): Riviersonderend Mts, (—BA), Ellis 5561.

Group 2B

This group includes all those species with linear glands but without swollen villous tiller bases. Morphologically and ecologically this group is exceedingly diverse with summer and winter rainfall species, annual and perennial taxa, as well as awned and unawned spikelets. It therefore appears to be a heterogeneous assemblage of taxa but the leaf anatomy, which is remarkably consistent throughout, suggests that this group is indeed a natural grouping. Apart from the unique linear gland type shared with Group 2A, the anatomy is characterized by distinctly tapering leaf margins, the extreme situation being where the margin is a narrow pointed projection. This structure is associated with mesic anatomy rather than the sclerophyllous-like anatomy which occurs in Group 2A.

Although the anatomy is undoubtedly of the mesic type, it is somewhat intermediate in some taxa and the chlorenchyma tends to be rather compact and may consist of larger, angular cells with a reduced air space system. The outer parenchyma sheath cells are generally conspicuous, containing no chloroplasts. Abaxial stomata may be irregular in occurrence or even absent. They may also be deformed in shape.

Linear leaf glands are restricted to this group in *Pentaschistis* (except for *P. velutina* of Group 2a) but also occur on the leaf blades in *Prionanthium* (Ellis 1989). Linear glands also occur on the pedicels and inflorescence rachis and branches in other taxa of Group 2A. This gland type appears to be the primitive state from which the elongated sessile, clavate and sunken types may have arisen (Linder *et al.* 1990).

It is of interest to note that some species with elongated sessile glands also share the tapering type of leaf margin and conspicuous parenchyma sheath cells. Examples are *P. pallida* forms D & G (Group 1B), and *P. natalensis*, *P. borussica* and rarely *P. setifolia* and possibly *P. ampla* (Group F). These taxa may be better accommodated in Group 2B or in a group very close to it, as this arrangement would also reflect the phylogeny of the various gland types.

The relationships of Group 2B, therefore, appear to be closer to several Group 1 taxa than to Group 2A. The transfer of Group 2B to Group 1 and its reconstitution including all species with sessile elongated glands, tapering leaf margins and conspicuous bundle sheath cells appears to reflect evolutionary lineages better than does the present arrangement. Groups 2A and 2B, which share sessile linear glands, do not appear to be closely related. The fact that this very unusual gland type also occurs in *Prionanthium* seems to support this contention and the separation of Groups 2A and 2B into different major species groups appears to be justified on this basis.

36 *P. trisetata* (Thunb.) Stapf
pp. 220–223 (Linder & Ellis 1990a: 69)

A curious obligate annual, the only annual species in Group 2 and the eglandular Groups 3–6, *P. trisetata* is restricted to Coastal Fynbos on acidic sandy soils on the lowlands from Cape Town northwards as far as Clanwilliam. It is a rare species due to the fact that it is usually present in the vegetation only in the first year after fire. Fire intervals in this vegetation may be in excess of 20 years, so this species is rarely collected. *P. trisetata* apparently survives this protracted interfire period as seed (Linder & Ellis 1990b).

The leaf anatomy of *P. trisetata* conforms closely to that characteristic of this group. Linear glands are visible on the leaf blades of all specimens examined, either in trans-section (Figure 36.1) or on the abaxial epidermis under transmitted light (Figure 36.2). Robbertse (1959) illustrates sessile linear glands for this species but referred to them as short epidermal cells. This gland type is not visible with the SEM (Figure 36.3). The marginal linear glands are 3- or 4-seriate (Figures 36.1B, C, D; 36.2A) whereas those located abaxially are usually only uniseriate (Figure 36.2E, F). The length of individual glands varies from six cells to more than 25.

The markedly tapering leaf margin, which is diagnostic for Group 2B, is not well developed in *P. trisetata*. There is, nevertheless, a definite decrease in the leaf thickness laterally to the ultimate vascular bundle (Figure 36.1). The margin itself is therefore, thinner than even the lateral parts of the lamina. Linear gland cells, which may be twice as large as normal epidermal cells, are usually evident in the extreme margin of the leaf blades (Figure 36.1B, C, D).

The chlorenchyma in most representatives of this species is very diffuse with an extensive air space system (Figure 36.1A–D). Very little sclerenchyma tissue is developed and only small strands are present. This lack of secondary cell walls and supporting tissues is consistent with the annual habit of this species where vegetative plant parts are only short-lived and thus not robustly constructed.

The epidermis has distinctive elongated rectangular long cells with sinuous walls (Figure 36.2A–E). Dome-shaped stomata are common as are microhairs. Basal and distal cells are more or less equal in length and the distal cell tapers noticeably (Figure 36.3C, D). The presence of macrohairs is variable, but when present they are of a distinctive type with the long hairs being soft and flexible and the base is inserted between two epidermal cells, one of which appears to be inflated (Figure 36.2B, C, D).

The undoubted resemblance between the anatomy of *P. trisetata* and that of all the species of *Prionanthium* (Ellis 1989) must be mentioned. These species share linear glands in the leaf margin (*Prionanthium* does not have abaxial linear glands), a tapering margin, similar adaxial ribs and furrows, chlorenchyma, microhairs, macrohairs, stomata and intercostal long cells. *Prionanthium*, however, has well differentiated stalked glands on the glumes (Davidse 1988) and, therefore possesses the diagnostic characters of both Groups 1 and 2 of *Pentastchistis*.

One specimen of *P. trisetata* (Ellis 5783) differs substantially in leaf anatomy from that described above and warrants further discussion. The chlorenchyma is much denser and there are conspicuous adaxial ribs with well-developed adaxial sclerenchyma girders (Figures 36.1E, F; 36.2F). The margin is in the form of a narrow projection and abaxial stomata are few in number. All these features are identical to those found on *P. rosea* subsp. *purpurascens* (Figures 37b.1; 37b.2), a closely related weakly perennial species which flowers in the second year after fire. It may be significant that this specimen of *P. trisetata* with this atypical anatomy was collected at precisely the same locality as several of the typical specimens of this species (Ellis 5421, 5422, 5423) except that it was collected a year later, two years after the burn. *P. trisetata* was very common in the first post-fire season but only a few isolated individuals were present in the second season. It seems more than coincidental that this specimen resembles the biennial *P. rosea* subsp. *purpurascens* so closely in leaf anatomy, although the plant itself shows no signs of being biennial. Further studies on the phenology and reproductive biology of this very interesting species are needed in order to understand its taxonomic interrelationships but this observation does strongly suggest that the affinities of *P. trisetata* are very close to *P. rosea* subsp. *purpurascens*.

SPECIMENS EXAMINED

CAPE.—3118 (Vanhynsdorp): Clanwilliam Dist., between Brakvlei and Nardouskloof, (–DD), Ellis 5421, 5422, 5423. 3119 (Calvinia): Lokenberg, (–CA), Acocks 17279. 3218 (Clanwilliam): Clanwilliam Dist., Nardouskloof, (–BB), Ellis 5783; Olifants River Mts, Marcuskraal, (–BD), Ellis 5426, Bo-Swartberg Farm, Ellis 5429.

37 *P. rosea* Linder
(Linder & Ellis 1990a: 70)

A weak perennial which flowers in the second year after fire, *P. rosea* frequents rather xeric mountain habitats, usually on dry sandy flats. It may completely dominate the vegetation in the second post-fire year but appears to be absent at all other times in the widely spaced fire cycle. As a result it is not often collected and, until recently, its distinctness was not appreciated.

This species includes a wide range of morphological variation, reflecting the habitats of individual plants but some is also clearly geographical. Two subspecies are recognised.

37a *P. rosea* Linder subsp. *rosea*
pp. 223–225 (Linder & Ellis 1990a: 71)

The population of *P. rosea* occurring on the suurvlakte of the plateau above Porterville is consistently different from the rest of the variation exhibited by this species. Subsp. *rosea* has a caespitose habit, setaceous leaves and a more compact inflorescence than the rest of the species.

Anatomically the leaves of subsp. *rosea* are narrow and tightly inrolled (Figure 37a.1). Adaxial ribs and furrows and sclerenchyma girders are well developed, the mesophyll is compact with limited air spaces only at the

bases of the furrows and the cuticle is thick. The epidermis has short long cells with thickened anticlinal walls, few microhairs but no other epidermal appendages (Figure 37a.2). These are typically xerophytic modifications but the large number of abaxial stomata are usually not associated with xeric anatomy.

The leaf margins are not typical of those of Group 2B in that they do not taper into a distinct projection and lack linear gland cells. Linear glands are, however, present on the abaxial costal zones (Figure 37a.2A–C). Sometimes they may be few in number and then the glands themselves are much shorter, consisting of four or five cells (Figure 37a.2D), thus resembling those of *P. velutina* (Figure 33.2) of Group 2A.

This taxon undoubtedly belongs in this linear gland group and is informative as to the degree of modification possible in the mesic leaf type. Although the leaf blades are clearly acicular, they can be assigned to this anatomical type on the basis of the mesophyll tissue and due to the presence of the linear glands.

SPECIMENS EXAMINED

CAPE.—3319 (Worcester): Porterville Mts, Suurvlak Farm, (–AA), *Ellis* 5483, 5793, 5797.

37b *P. rosea* Linder subsp. *purpurascens* Linder pp. 226–228 (Linder & Ellis 1990a: 72)

This subspecies is found from the Hottentots Holland Mountains to the Cederberg. It includes a wide range of variation, from flat cushions at high altitudes to caespitose tufts in more mesic localities.

The leaf blades are of the expanded type (although they may be variously infolded) (Figure 37b.1A, B, D), the margin is a definite narrow projection (Figure 37b.1C, E–G), adaxial ribs and furrows are well developed with adaxial sclerenchyma girders and strands more prominent and the chlorenchyma tends to resemble the compact type, the individual cells being angular but rather large. Linear glands are visible in the margin and opposite the larger bundles. This transectional anatomy is typical of that diagnostic for Group 2B and closely resembles that of *P. pseudopallescens* (Figure 38.1) and *P. pallescens* (Figure 39.1).

The epidermal pattern of subsp. *purpurascens* is rather uniform but costal and intercostal zones are distinguishable. Linear glands are located on the costal zones (Figure 37b.2B–E) and in the leaf margin (Figure 37b.2F). No macrohairs or prickles occur and microhairs are common with a short, tapering distal cell (Figure 37b.3B). Dome-shaped stomata do occur but their presence is variable and they are sometimes absent (Figure 37b.2A, B). Their presence is linked to habitat and they do not occur in specimens from higher more xeric localities.

P. rosea subsp. *purpurascens* possesses all the diagnostic features of Group 2B. Although it is morphologically rather variable the anatomy is remarkably uniform, even in plants with widely differing growth forms. Its

recognition as a new taxon is fully supported by the anatomical evidence as is its placement in this species group with linear glands.

SPECIMENS EXAMINED

CAPE.—3218 (Clanwilliam): Piketberg Mtn, Avontuur, (–DC), *Ellis* 5800. 3219 (Wuppertal): Cederberg Mts, Sneekop Peak, (–AC), *Ellis* 5510, 5514; Middelberg North Peak, *Ellis* 5580, 5582, 5586, 5789, 5790. 3319 (Worcester): Hex River Mts, Milner Peak, (–AD), *Ellis* 5532, 5535.

38 *P. pseudopallescens* Linder pp. 229–231 (Linder & Ellis 1990a: 72)

P. pseudopallescens is a weak perennial flowering in the second post-fire season in the mountains of the south-western Cape, from the Hex River Mountains to the Koue Bokkeveld Mountains. In contrast to *P. rosea* subsp. *purpurascens*, *P. pseudopallescens* prefers damp sandy soils along streams or seepages. These two species are often associated together as they have the same post-fire flowering biology.

Anatomically *P. pseudopallescens* displays all the diagnostic features of Group 2B: the leaf margin is a distinct projection and contains linear glands (Figure 38.1), the mesophyll tissue is rather compactly arranged and the outer bundle sheath cells are conspicuous due to the absence of chloroplasts (Figure 38.1B–F), the occurrence of abaxial stomata is irregular with some specimens lacking them altogether (Figure 38.2) and abaxial microhairs are usually present (Figure 38.3). All these attributes indicate affinities with the Group 2B taxa and *P. pseudopallescens* appears to be very closely related to *P. trisetata*, *P. rosea* and *P. pallescens*.

Differences between *P. pseudopallescens* and *P. rosea* subsp. *purpurascens* are the general absence of abaxial linear glands in most *P. pseudopallescens* specimens (Figure 38.2C–F), although they are common on the leaf margins, and the presence of macrohairs on *P. pseudopallescens*. *P. rosea* subsp. *purpurascens* also has larger adaxial ribs than *P. pseudopallescens*. *P. pseudopallescens* and *P. pallescens* are very similar in transectional anatomy except that the marginal linear glands in *P. pallescens* are not as well developed or as common (Figure 39.1). The epidermis of *P. pallescens* also lacks stomata, macrohairs and microhairs (Figure 39.2). Another difference is that the long cell walls are not sinuous like those in *P. pseudopallescens*. The adaxial microhairs of *P. pallescens* differ in having a very small distal cell (Figure 39.3E, F) and the whole hair is longer and thinner than those of *P. pseudopallescens* (Figure 38.3F).

P. pseudopallescens, therefore, links the large, strongly perennial *P. pallescens* to the shorter-lived, smaller taxa such as *P. rosea* and *P. trisetata*. This relationship is supported by the shared possession of the distinctive diagnostic criteria for this group, albeit in slightly modified form in each of the taxa.

SPECIMENS EXAMINED

CAPE.—3319 (Worcester): Porterville Mts, Groot Winterhoek Wilderness Area, (–AA), *Ellis* 5796; Hex River Mts, Milner Peak, (–AD),

39 *P. pallescens* (Schrad.) Stapf pp. 232–235 (Linder & Ellis 1990a: 74)

A tall caespitose perennial from the mountains of the south-western Cape from Worcester to the Hottentots Holland Mountains and the Peninsula, *P. pallescens* is generally found at lower altitudes in slightly disturbed sites.

The leaf blades are 8–10 mm wide, expanded but exhibiting various degrees of infolding and inrolling in response to prevailing moisture conditions. In transectional anatomy *P. pallescens* conforms in all respects to the anatomical type characteristic of Group 2B (Figure 39.1) and this transectional anatomy is remarkably uniform throughout the large and fully representative sample studied. The specimens illustrated by Robbertse (1959) support this observation.

The narrow projecting margin, adaxial ribs and furrows, conspicuous outer bundle sheath cells devoid of chloroplasts and the relatively compact mesophyll tissue are features which serve to strongly link this species to Group 2B. The only significant transectional differences between *P. pallescens* and *P. pseudopallescens* (Figure 38.1) and *P. rosea* subsp. *purpurascens* (Figure 37b.1) are general absence of marginal linear glands and larger abaxial epidermal cells in *P. pallescens*.

The abaxial epidermis of *P. pallescens* differs considerably from these other two taxa. The entire abaxial epidermis consists of large intercostal long cells (as seen in transverse section) and costal and intercostal zones are not differentiated (Figure 39.2). These long cells tend towards a fusiform shape, do not have sinuous walls and are separated by one or two tall and narrow short cells—features not present in *P. rosea* subsp. *purpurascens* (Figure 37b.2) or *P. pseudopallescens* (Figure 38.2). No stomata or costal silica bodies are present on the abaxial epidermis of *P. pallescens* and macrohairs, microhairs and linear glands are very rare. When present, the macrohairs are very thin and flexible arising from a small cushion base (Figure 39.2E). Microhairs are elongate with a very short distal cell (Figure 39.2F) and the linear glands are uniseriate with rather small cells (Figure 39.2F).

The adaxial microhairs also differ from those of *P. pseudopallescens* and *P. rosea* subsp. *purpurascens* in that they are long and thin with a very small distal cell (Figure 39.3E, F). This hair structure is very similar to that of *P. aurea* subsp. *pilosogluma* (Figure 40b.3E–H) also of Group 2B. *P. aristoides* (Figure 32.4B, D, F) and *P. velutina* (Figure 33.3D, F) of Group 2A as well as many of the eglandular *Pentastichis* species such as *P. pyrophila* (Figure 44.3G, H), *P. curvifolia* (Figure 56.3C, F), *P. pungens* (Figure 57.3C, F) and *P. eriostoma* (Figure 67.4C, F) also have this type of adaxial microhair. Similar microhairs are also found on some glandular species of Group 1F, examples being *P. natalensis* (Figure 22.3D), *P. oreodoxa* (Figure 23.4F) and *P. ampla* (Figure 25.2C, D).

The adaxial microhairs of *P. setifolia* and *P. glandulosa* are somewhat intermediate with the distal cell being considerably longer and the hair much thicker. This very unusual type of microhair, therefore, occurs on both glandular and eglandular *Pentastichis* species and appears to be of little taxonomic significance.

Although interpretation of the taxonomic importance or otherwise of these unique microhairs is difficult, their presence in *P. pallescens* serves to demonstrate the strong link between those Group 2B species with distinctly tapering margins and linear glands but lacking microhairs with short distal cells (*P. trisetia*, *P. rosea* and *P. pseudopallescens*) and those species without such obviously tapering margins and linear glands and with very elongate microhairs with minute distal cells. These taxa also belong to Group 2B (*P. aurea*) as well as Group 1 (*P. pallida* forms D & G, *P. natalensis*, *P. ampla* and *P. borussica*). All these species appear to be closely related and *P. pallescens*, therefore, is central to a better understanding of relationships in the genus.

SPECIMENS EXAMINED

CAPE.—3318 (Cape Town): Table Mtn, (—CD), Ellis 5572, 5573, Linder 4338, Kirstenbosch, Ellis 2309; Jonkershoek, (—DD), Ellis 2250, 2251. 3319 (Worcester): Franschhoek Pass, (—CC), Ellis 5537; Du Toitskloof Pass, Ellis 5978. 3418 (Simonstown): Hottentots Holland Mts, (—BB), Ellis 2271, 2272, 2276, 2277.

40 *P. aurea* (Steud.) McClean (Linder & Ellis 1990a: 75)

P. aurea is an awnless, perennial, caespitose species with linear glands usually restricted to the pedicels. The distribution range extends from the western and southern Cape to the Natal Drakensberg Mountains. A wide range of spikelet and plant size is included in this taxon with the western and southern plants being small with small spikelets, whereas the Drakensberg plants form large tussocks with the spikelets at least a third longer. In the eastern Cape Province the plants and the spikelets are intermediate between these two extremes and, consequently, they are treated as two subspecies.

40a *P. aurea* (Steud.) McClean subsp. *aurea* pp. 236–238 (Linder & Ellis 1990a: 76)

Widespread in the winter rainfall areas of the Cape from Namaqualand to Uitenhage, the plants and the spikelets of *P. aurea* subsp. *aurea* are generally smaller than those of subsp. *pilosogluma*. Spikelet size and shape is very similar to that of *P. ampla* of Group 1F, and consequently these two taxa may be difficult to separate.

Anatomically subsp. *aurea* differs somewhat from the preceding taxa of Group 2B. Linear leaf glands were not observed and the leaf margin is not a narrow projection (Figure 40a.1), although it is distinctly tapering. The chlorenchyma is diffuse although rather compactly arranged (Figure 40a.1B) and the outer bundle sheaths do not contain chloroplasts, being conspicuous as is the case in Group 2B.

Zonation of the abaxial epidermis is clearly differentiated with the costal silica bodies being dumbbell-shaped (Figure 40a.2). The intercostal long cells are fusiform in shape and the anticlinal walls are only very slightly sinuous (Figure 40a.2). Abaxial microhairs are generally present, these having distal cells which are longer than the basal cells (Figure 40a.3B). This distal cell is much shorter in the adaxial microhairs (Figure 40a.3D).

Abaxial stomata are common on most specimens although they may be rare and irregular in occurrence (Figure 40a.2D). A large proportion of these abaxial stomata are deformed, often with two or more adjacent stomata in a file being fused (Figure 40a.2B, C). Similar stomatal deformities were also observed on *P. pallida* form D (Figure 7d.2B), *P. natalensis* (Figure 22.2E) and *P. ampla* but they are most frequent on *P. aurea* subsp. *aurea*. Deformed stomata were not observed on subsp. *pilosogluma* (Figure 40b.2).

Marginal leaf glands, although very rare, were observed. These are not typical of the linear gland type, being discrete elliptical groups of cells only slightly raised above the general epidermal level. They thus appear to be intermediate between the linear gland type and the type illustrated for *P. pallida* form G (Figure 7g.2A, B), the elongated sessile type. Similar abaxial glands are sometimes present on subsp. *pilosogluma* as illustrated in Figure 40b.2F.

The leaf anatomy of *P. aurea* subsp. *aurea*, therefore, appears to be more similar to that of *P. pallida* forms D and G, *P. natalensis* and *P. ampla* (particularly the eastern form), all of which belong to Group 1, than it is to the remainder of Group 2B. However, shared characters such as tapering margins and colourless bundle sheath cells, do support the widening of the concept of Group 2B to include all those taxa without stalked glands i.e. elongated sessile as well as sessile linear glands. It is also possible that the sunken, crateriform type of gland should also be included in this assemblage.

SPECIMENS EXAMINED

CAPE.—3319 (Worcester): Franschoek Pass, Adolfskop, (—CC), Linder 4604. 3322 (Oudtshoorn): George Dist., Montagu Pass, (—CD), Ellis 5822. 3418 (Simonstown): Betty's Bay, (—BD), Ellis 5539, 5570.

40b *P. aurea* (Steud.) McClean subsp. *pilosogluma* (McClean) Linder
pp. 239–241 (Linder & Ellis 1990a: 76)

This subspecies is found in temperate habitats in the mountains of the summer rainfall region of southern Africa, from the eastern Cape to the northern Natal Drakensberg. It occurs in both cave sandstone and basalt soils, especially in moist sites.

The leaf anatomy of subsp. *pilosogluma* conforms with that of the Group 2B species in most respects. The characteristic narrow, tapering margin is always present (Figure 40b.1A, B) and the outer bundle sheath cells are devoid of chloroplasts. The chlorenchyma may be rather compact

(Figure 40b.1B, C, E) but is often of the diffuse type (Figure 40b.1D, F, G).

Intercostal long cells, although not very long, tend to the fusiform type and are separated by tall and narrow short cells (Figure 40b.2), resembling the situation in *P. pallescens* (Figure 39.2). Abaxial stomata are rare and microhairs appear to be absent. Adaxial microhairs are consistently elongated with very small distal cells (Figure 40b.3E–H).

The glands on subsp. *pilosogluma* are of particular interest. Linear glands are seldom present in the margin and then are barely visible, being uniseriate and the gland cell is not much larger than the normal epidermal cells. Unusual elliptical glands are very rare on the abaxial epidermis (Figure 40b.1G). These glands are not uniseriate but are discrete elliptical groups of cells as seen in surface view (Figure 40b.2F). This gland type occurs on *P. aurea* subsp. *aurea* as well as two specimens of *P. setifolia* (Figure 24.4G). This same gland type is also more frequently found on the ribs of the adaxial surface of subsp. *pilosogluma* (Figure 40b.1D, F, G), with the outlines of the small gland cells visible under the SEM (Figure 40b.3D). The adaxial location of these glands seems to be unique in the genus. They were also observed on two specimens of *P. setifolia* (Figure 24.3H), although the identification of these two specimens from Naudesnek needs verification. They were also observed on *P. borusica* (Figure 21.1A, B).

This unraised, elliptical gland structure may be a modification of the linear gland type and appears to be intermediate between the sessile and the sunken types. This observation supports the grouping together of all those glandular species without stalked glands and the relationships of the species with sunken glands (Group 1F) appear to be closer to this assemblage rather than to species with stalked glands.

SPECIMENS EXAMINED

O.F.S.—2828 (Bethlehem): Witsieshoek Dist., Mont-aux-Sources, Sentinel Peak, (—DB), Ellis 3159, 5730.

NATAL.—2929 (Underberg): Cathedral Peak, Organ Pipes Pass, (—AA), Ellis 5716; Highmoor State Forest, (—BC), Ellis 3162; Sani Pass, (—CB), Ellis 5708, Du Toit 2307, Killick & Vahrmeijer 3807; Garden Castle, Mzimkhulu Wilderness Area, (—CC), Ellis 5699.

CAPE.—3324 (Steytlerville): Groot Winterhoek Mts, Cockscomb Peak, (—DB), Ellis 5616, 5617.

Group 3

This group, together with Groups 4–6, includes all the eglandular species of *Pentastichis*. This absence of glands is generally associated with the sclerophyllous type of leaf anatomy and the taxa of Group 3 generally have the typical sclerophyllous anatomical type.

Sclerophyllous leaf anatomy is discussed in the introduction and by Ellis (1988a) and Linder & Ellis (1990b). This anatomical type is associated with tough, long-lived leaf blades, an unusual situation in grasses where above-ground

organs are generally annual, remaining alive during the growing season only and thereafter senescing. This sclerophyllous type appears to be an adaptation to nutrient deficiencies which generally occur in soils derived from Table Mountain Sandstone and which are widespread in the fynbos biome of the winter rainfall region of the Cape Province. The fynbos vegetation generally is characterised by being sclerophyllous and the eglandular species of *Pentaschistis* are no exception and this life-form may ensure the most efficient use of scarce soil nutrients. The taxa of this group, therefore, are most common on infertile sands in the mountains of the south-western Cape but are rare on more fertile soils.

Structurally this leaf type is characterised by a very compact mesophyll tissue and the chlorenchyma cells are small and isodiametric in transectional shape. Consequently, the intercellular air space system is very reduced or even apparently absent as seen in cross section. The vascular bundles are relatively close together, much closer than those of *Pentaschistis* species with the mesic leaf type, and are always associated with extensive supporting tissue which may even occur between the bundles beneath the abaxial epidermis. The leaves are often setaceous and tightly inrolled, this being associated with prominent adaxial ribs and deep, cleft-like furrows. The cuticle is generally thick.

The epidermal pattern also differs considerably from that typical of the mesic type. Zonation is often not evident, particularly on permanently infolded leaves with hypodermal sclerenchyma development. Abaxial stomata are usually absent on this leaf type as well. When epidermal zonation is developed the costal zones are typically wider than the intercostal zones due to the presence of large abaxial sclerenchyma girders. The intercostal long cells usually have thickened, sinuous anticlinal walls, which are often deeply undulating. Abaxial microhairs are often lacking on this leaf type as are stomata.

This typical sclerophyllous type is contrasted with the mesic type in the introduction. The generalized description of this leaf type is also subject to much modification in nature and variation in all the sclerophyllous attributes does occur. This is not the case with the compact type of mesophyll tissue, however. The compact tissue can consistently be used to separate this leaf type from the mesic type, even in mesic leaves which superficially resemble the sclerophyllous type in being permanently inrolled or infolded.

In the eglandular *Pentaschistis* species of Groups 3–6, two types of chlorenchyma are found: i) small, isodiametric cells with centrally located vacuoles which are typical of the sclerophyllous leaf type; ii) larger cells also with angular cell walls but vacuoles are usually not distinguishable. This type of mesophyll appears to be a xerophilic or cryophilic adaptation of the mesic type.

These two mesophyll types are generally accommodated separately in Groups 3A and B and may be taxonomically meaningful.

Group 3A

These are eglandular *Pentaschistis* species with branching culms and with few-flowered inflorescences. The sclerophyllous type of anatomy is characteristic of this group. Chlorenchyma of small cells with clearly defined angular walls and with round, centrally located vacuoles visible in all cells is the most common and is present in all taxa except *P. montana* and *P. rigidissima*. *P. pusilla* has typical mesic type mesophyll and appears to be misplaced in this group.

The mesophyll of these exceptions closely resembles that of most of the Group 3B taxa and their transfer to this subgroup is suggested by the leaf anatomy. By the same token *P. tysonii*, *P. holciformis* and *P. praecox* do not appear to be correctly placed in this latter group of species and may be better accommodated in, or close to, Group 3A. This rearrangement will result in uniformity of chlorenchyma structure in Groups 3A and 3B.

Papillate adaxial epidermides, microhairs with the distal cell not considerably shorter than the basal cell and dumbbell-shaped silica bodies would also be associated with this uniformity in chlorenchyma tissue for Group 3A (with *P. pyrophila* being the only exception). Groupings based on this combination of anatomical characters appear to be more natural than those currently used and the morphological implications of a realignment based on this evidence should be considered.

41 *P. colorata* (Steud.) Stapf pp. 242–248 (Linder & Ellis 1990a: 77)

This species is morphologically variable, a situation which is also evident in the leaf anatomy. *P. colorata* can be considered as being at the centre of a species complex and segregating neighbouring taxa is difficult and somewhat arbitrary. Notwithstanding these practical difficulties, the leaf anatomy fully supports the concept of this species, its closest allies being *P. tortuosa* and *P. alticola* with *P. elegans*, *P. malouinensis* and *P. calcicola* being slightly further removed.

It is of interest that *P. colorata* generally occurs at altitudes intermediate between *P. tortuosa* (at lower altitudes) and *P. alticola* (above 1 000 m). Similarities with both these segregates are evident in the fully representative anatomical sample of *P. colorata* studied, implying that *P. colorata* may be too widely delimited as here circumscribed but illustrating how difficult the separation of these taxa is in practice.

P. colorata always has a permanently infolded, setaceous leaf (Figure 41.1) with the outline varying from solid, rounded to elliptical to hollow, canaliculate. Both leaf types are illustrated by Robbertse (1959). These differences in shape do not appear to be geographically or ecologically based and different leaf outlines occur in the same populations e.g. *Ellis* 2495 (Figure 41.1A) and *Ellis* 2498 (Figure 41.1F) were both collected on the Buffelshoek Pass on the Koue Bokkeveld Mountains. A similar situation

was also observed in the Jonkershoek, Tradouw's Pass and Garcia's Pass collections, all of which had both round and canaliculate outlines. Those from the Hottentots Holland Mountains were similar except that only rounded and elliptical outlines were observed.

The canaliculate outline is virtually identical to that of *P. tortuosa* (Figure 42.1) except that in this species the blades tend to be much wider. These specimens with this type of leaf outline, therefore, tend to intergrade anatomically with *P. tortuosa*. This applies more specifically to leaves without abaxial papillae (Figure 41.1H, I). These unique structures do not occur on *P. tortuosa* but are present on *P. alticola*, which also has a narrow but canaliculate type outline (Figure 43.1A). This clearly illustrates the indistinct interface between *P. colorata* and these two closely related taxa. No specimens with rounded or elliptical leaf outlines were assigned to these neighbouring taxa and this type of outline can be considered as being central to *P. colorata*.

Features of the transectional anatomy of *P. colorata* which are either diagnostic or taxonomically significant are the abaxial epidermal cell size, the papillate adaxial epidermal cells, the arrangement of the first order bundles and the vacuolate, isodiametric chlorenchyma cells. The abaxial intercostal long cells are much larger than the costal long cells as well as being larger than the abaxial epidermal cells (Figure 41.2). This configuration is restricted to the *P. colorata* complex of Group 3A but does not occur in other taxa of this group such as *P. pyrophila*, *P. montana*, *P. rigidissima* or *P. pusilla*.

Similarly the sequence of lateral first order vascular bundles, the chlorenchyma cell structure, papillate adaxial epidermis and microhair shape serve to unify the *P. colorata* group of species and to exclude the other Group 3A taxa. This distinctive character combination also suggests affinities with *P. tysonii*, *P. holciformis* and *P. praecox* of Group 3B. Furthermore the overall anatomy of all these taxa resembles that of *Merxmüllera stricta* and its allies very closely (Ellis 1980b, 1981b), much more so than any other *Pentastichis* species. This appears to imply that realignment of genera in the Arundineae is needed to reflect these strong anatomical similarities.

The abaxial epidermis of the *P. colorata* complex is also very characteristic, differing considerably from that of any of the other species groups. The dumbbell-shaped silica bodies are unusual in the eglandular *Pentastichis* species, as is the distinct epidermal zonation (Figures 41.3; 41.4). Abaxial microhairs, which are unusually common, are also distinctive with the slightly tapering distal cell being equal to or longer than the basal cell (Figures 41.5B, F; 41.6B). The adaxial microhairs also do not have a noticeably shorter distal cell (Figure 41.5D, H). This hair type differs considerably in basic structure from that of all other *Pentastichis* species and resembles that of *Merxmüllera stricta* and its allies very closely.

The abaxial cuticular papillae, a very unusual characteristic in the Arundinoideae, are only known in *P. colorata* (Figures 41.3; 41.5) and *P. alticola* (Figures 43.1; 43.2). These papillae are common on *P. colorata* but are

only found on the intercostal zone on either side of the median vascular bundle. They are often very difficult to see in epidermal scrapes and do not occur on all leaves or specimens. Their presence also does not seem to be geographically linked, being present and absent in samples from the same populations.

The ultrastructure of the adaxial epidermis of the *P. colorata* group of species differs substantially from that of all other *Pentastichis* species in that the long cells have inflated periclinal walls (Figures 41.5C, G; 41.6C, E). These inflated papillae are particularly well developed on the interstomatal cells and tend to overarch the stomata which are sunken between these cells. This type of adaxial epidermal configuration also occurs in *Merxmüllera stricta* and its relatives as well as *P. tysonii*, *P. holciformis* and *P. praecox*.

The leaf anatomy, therefore, suggests that *P. colorata* and its relatives belong to a very distinct group exhibiting strong links to *M. stricta* and its allies. *P. colorata* certainly is rather far removed from the glandular *Pentastichis* species as well as the remaining eglandular species of Groups 3 and 4. This evidence associating the *P. colorata* complex with *M. stricta* and its allies is certainly not suggested by any morphological characters as presently interpreted. The resolution of this apparent impasse between the anatomical and morphological indications calls for a comprehensive worldwide phylogenetic study of the entire tribe.

SPECIMENS EXAMINED

CAPE.—3219 (Wuppertal): Citrusdal, Buffelshoek Pass, Kouebokkeveld Mts, (—CA), *Ellis* 2496+; 2498*+; 3318 (Cape Town): Table Mtn, (—CD), *Linder* 4341; Jonkershoek, Witbrug, (—DD), *Ellis* 2230*+, Jakkalsvlei, *Ellis* 2230+; 2232*+, Swartboskloof, *Ellis* 2259*. Heuningvlei, *Ellis* 2264*+. 3319 (Worcester): Ceres, Gydo Pass, Schurftieberg, (—AB), *Ellis* 2485; Hex River Mts, Milner Peak, (—AD), *Ellis* 5536+; Franschoek Pass, (—CC), *Ellis* 2350*+, 2352+. 3320 (Montagu): Barrydale, Tradouw Pass, (—DC), *Ellis* 649*+, 1200+, 1201*+, 1680*+, 1681*+, 1682*+; Langeberg, Grootvadersbos, (—DD), *Ellis* 5546, 5551. 3321 (Ladismith): Langeberg, Garcia's Pass, (—CC), *Ellis* 2539+, 2541+, 2545*. 3322 (Oudtshoorn): Outeniqua Mts, Robinson Pass, (—CC), *Ellis* 2585. 3418 (Simonstown): Cape Peninsula, Scarborough, (—AB), *Ellis* 5438; Hottentots Holland Mts, Sugarloaf Peak, (—BB), *Ellis* 2269, 2270, 2274+, 2279, 2281, Sir Lowry's Pass, *Ellis* 2295, 2296. 3419 (Caledon): Groenlandberge, Viljoen's Pass, (—AA), *Ellis* 5445*+; Riviersonderend-berge, Die Galg, (—BA), *Ellis* 5563, 5805; Viljoenshof, (—CA), *Ellis* 5593.

* specimens with canaliculate leaf blades.
+ cuticular papillae on the abaxial epidermis.

42 *P. tortuosa* (Trin.) Stapf pp. 249–251 (Linder & Ellis 1990a: 78)

P. tortuosa is very similar to *P. colorata*, the herbarium specimens being particularly difficult to tell apart. *P. tortuosa* is distinctive in the field due to its size, brown drooping inflorescences and caespitose tussocks. It is common at lower altitudes from the Cape Peninsula eastwards as far as Uniondale. It may be sympatric with *P. colorata* although this species is more common higher up mountain slopes.

The affinities of *P. tortuosa* are undoubtedly very close to *P. colorata* and these two taxa belong to the same species complex. This is fully supported by the leaf anatomy as *P. tortuosa* has canaliculate leaves virtually identical to those of many *P. colorata* specimens, as can be seen by comparing Figures 41.1H, I with 42.1A, D and Robbertse (1959). Leaf width in *P. tortuosa* tends to be much greater (Figure 42.1A) than in *P. colorata* and generally more than nine vascular bundles are present—11, 13, 15, 17, 19 or 21. However, specimens with narrow inrolled leaves do occur (Figure 42.1D). In these examples the leaf blade outlines are identical to those of the canaliculate *P. colorata* specimens, even as regards the number of vascular bundles. The wider *P. tortuosa* leaves differ from the *P. colorata* leaves only in the number of vascular bundles in the blade, the configuration of all the other tissues and cells being identical. The only possible difference is the third order bundles which are interposed between the lateral first order bundles (Figure 42.1B, E).

Abaxial papillae were not observed on any *P. tortuosa* specimen although they were often associated with canaliculate leaves in *P. colorata* (see specimens examined in that species). However the correlation between papillate epidermis and the canaliculate leaf type is not perfect in *P. colorata* so this character cannot be used to separate these two species.

The canaliculate leaf type in *P. colorata* differs significantly from the rounded and elliptical leaf outlines (Figure 41.1) and the variation between these two basic outlines is not continuous, no leaves which can be considered as being intermediate were observed. The logical solution to this excessive degree of variation in *P. colorata* is to suggest the removal of all those specimens with the canaliculate type of leaf to *P. tortuosa*. However, this will lead to papillae being shared by both species and many of the *P. colorata* specimens with canaliculate leaves typically have *P. colorata* morphology with few, larger spikelets on rather small plants. This shows clearly the difficulties involved in separating species in the *P. colorata* complex.

The epidermal anatomy of *P. tortuosa* (Figure 42.2) is also very similar to that of *P. colorata* although microhairs are much less common. When they do occur they are very similar to those of *P. colorata* (Figure 42.3D) with basal and distal cell of equal length (Robbertse 1959). Inflated papillae are found on the adaxial epidermis (Figure 42.3B, C) and are particularly well developed on the interstomatal long cells. This is also a very unusual feature shared with *P. colorata* and its allies as well as *Merxmüllera stricta* and its allies.

P. tortuosa is undoubtedly correctly placed in this species group and conforms in all respects to the anatomical diagnosis of Group 3A if *P. pyrophila*, *P. montana*, *P. rigidissima* and *P. pusilla* are excluded.

SPECIMENS EXAMINED

CAPE.—3318 (Cape Town): Table Mtn, (—CD), *Ellis* 2310, *Linder* 4340; Jonkershoek, Jakkalsvlei, (—DD), *Ellis* 2226, 2227, 2228, Swartboskloof, *Ellis* 2260, 2261, 3323 (Willowmore); Joubertina, (—AC), *Esterhuysen* 27320; Tsitsikama, (—DC), *Ellis* 5603, 3324 (Steytierville); Groot Winterhoek Mts, Cockscomb, (—DB), *Ellis* 5607.

43 *P. alticola* Linder

pp. 252, 253 (Linder & Ellis 1990a: 79)

A small, cushion-forming species from the Hex River Mountains to the southern Cederberg, *P. alticola* occurs above 1 000m, and appears to be a high altitude segregate of *P. colorata*.

All the diagnostic anatomical features of *P. colorata* are exhibited by *P. alticola*: abaxial cuticular papillae (Figure 43.1B, C); microhairs with distal and basal cells of equal length (Figure 43.1D, F); abaxial epidermal cells larger than the adaxial ones (Figure 43.1A); adaxial epidermal cells with inflated papillae (Figure 43.1E); compact chlorenchyma of isodiametric cells with central vacuoles (Figure 43.1A) and dumbbell-shaped silica bodies (Figure 43.1B, C).

Except for the much smaller size of the *P. alticola* leaves (compare the scales on Figure 43.1A ($\times 250$) with those on 41.1H, I ($\times 160$)), there is no difference in the leaf anatomy of these two species and the anatomical evidence fully supports the morphological indications of close ties between these taxa.

A form of *P. alticola* which has awnless lemmas is represented by several collections e.g. *Ellis* 5502. The anatomy of this specimen is illustrated in Figure 43.2, showing it to be very similar to typical *P. alticola* specimens, the only difference being the presence of abaxial cushion-based macrohairs (Figure 43.2A). Similar macrohairs are very common on *P. elegans* (Figures 50.1C; 50.2A, C) which also belongs to the *P. colorata* complex. This anatomy undoubtedly places these awnless specimens in the *P. colorata* complex and confirms the independent loss of awns in this species group. The placement of *P. malouinensis* in the *P. colorata* complex (Group 3A) is, therefore, supported by these observations on this unusual form of *P. alticola*. Some specimens of *P. pusilla*, which is also without awns (and only has one spikelet), also resemble this form of *P. alticola* very closely in leaf anatomy (Figure 49.1E, F). It seems as if these specimens would be better placed in *P. alticola* than in *P. pusilla*.

SPECIMENS EXAMINED

CAPE.—3219 (Wuppertal): Cederberg, Krom River Kloof, (—CB), *Esterhuysen* 17987, 3319 (Worcester): Hex River Mts, Milner Peak, (—AD), *Ellis* 5528; Groot Winterhoek Wilderness Area, Groenberg, (—CC), *Ellis* 5502 (awnless).

44 *P. pyrophila* Linder

pp. 254–257 (Linder & Ellis 1990a: 81)

P. pyrophila is a pyrophytic species of the mountains of the western and southern Cape Province. It only flowers after fire, and as fire intervals are widely spaced in the fynbos vegetation, this species is rarely collected. Thus, although it occurs from the Cederberg in the west to the Groot Winterhoek Mountains in the east, it has only recently been described. Being such a wide-ranging species it includes a wide range of morphological variation which is also reflected in the leaf anatomy.

Although the anatomy of *P. pyrophila* is variable, a group of anatomical characters in combination serve to distinguish this species from all the other taxa of Group 3A. In the leaf in transverse section these characters are (Figure 44.1): the sequence of arrangement of different orders of vascular bundle across the leaf blade, the development of a continuous abaxial hypodermal layer of fibres, vascular bundles with collenchyma sheath extensions gradually intergrading into the girders and the abaxial epidermal cells are all uniform in size and considerably larger than the adaxial epidermal cells.

The epidermis also has many distinguishing features (Figures 44.2; 44.3): abaxial zonation is not evident, the abaxial epidermis has a brick-work pattern with long cells alternating with cork-silica cell pairs, silica bodies are elliptical in shape, abaxial microhairs and stomata are absent (with one exception), adaxial microhairs are very long and thin with a minute distal cell, adaxial ribs with sharply pointed prickly hairs although these may vary in number.

None of these anatomical characteristics of *P. pyrophila* is shared with the *P. colorata* complex and there are no indications from the leaf anatomy of a close relationship between these two taxa. The placing of *P. pyrophila* in Group 3A appears to be artificial as it shares very little in common with the *P. colorata* species complex or with the other anomalous species in this group—*P. montana*, *P. rigidissima* or *P. pusilla*.

Notwithstanding the above, the leaf anatomy of *P. pyrophila* corresponds very closely with that of all the species of Group 4 (*P. curvifolia*, *P. pungens*, *P. acinosa*, *P. caulescens* and *P. scandens*) except that *P. pyrophila* does not display a tendency to have thick leaf margins, as do all these taxa of Group 4. *P. eriostoma* of Group 6 also has very similar leaf anatomy to *P. pyrophila* and these Group 4 species. A comparison of the anatomy of all these species reveals that they all share essentially the same type of basic anatomy characterized by the distinguishing features elucidated for *P. pyrophila* above.

In addition, this anatomical configuration is also very similar to that of *Pentameris longiglumis* (Ellis 1985b), *Pentameris macrocalycina* and *Pentameris obtusifolia* (Ellis 1985d). The leaf anatomy, therefore, suggests affinities between *Pentaschistis pyrophila*, the Group 4 *Pentaschistis* species and these *Pentameris* species.

The anatomy indicates, therefore, that this entire group of species should be accommodated together in a single supraspecific group. This implies that the present separation of *Pentaschistis* and *Pentameris*, based on the presence or absence of a terminal tuft of bristles on the ovary, is artificial. Studies are needed to establish whether further character correlations occur between all these species before taxonomic decisions can be taken. The anatomy of the leaf blade clearly shows that *P. pyrophila* is incorrectly placed in Group 3 of *Pentaschistis*.

SPECIMENS EXAMINED

CAPE.—3319 (Worcester): Hex River Mts, Milner Peak, (—AD), Ellis 5530, 5533. 3321 (Ladismith): Great Swartberg, Waboomsberg, (—BD),

Ellis 5618, 5623, 5626, Gamkaskloof road, Ellis 5629. 3419 (Caledon): Riviersonderend Mts, Wa-en-Osse Peak, (—BA), Ellis 5556, 5807, 5809.

45 *P. calcicola* Linder

(Linder & Ellis 1990a: 81)

This species is locally common on the coastal forelands of the Bredasdorp District. This is the only *Pentaschistis* species endemic to limestone although *P. cirrhulosa* and *P. pallida* form C are often found associated with calcareous and limestone substrates.

Two rather distinct forms occur within *P. calcicola*: the leaves are glabrous in one, and puberulous in the other. Associated with this are differences in spikelet size and inflorescence structure as well as different flowering times. As they are closely associated geographically, they are recognized as varieties until the relationship between them becomes clearer.

45a *P. calcicola* Linder var. *calcicola*

pp. 257–259 (Linder & Ellis 1990a: 83)

Several features of the leaf anatomy of this variety suggest affinities with the *P. colorata* complex. The mesophyll is compact with angular cells which are slightly larger than is usual in *P. colorata* and its close allies (Figure 45a.1A, B). First and third order vascular bundles alternate across the leaf width and abaxial sclerenchyma girders are well developed. The abaxial intercostal epidermal cells are considerably larger than the adaxial ones (Figure 45a.1) but these are not as papillate as in *P. colorata*.

The abaxial epidermis also resembles the *P. colorata* type in most respects although it does display several differences. Stomata are absent and no abaxial microhairs were observed (Figures 45a.2; 45a.3A, B). The intercostal long cells are rather short but retain the fusiform shape and sinuous walls of the *P. colorata* species group. The silica bodies are very variable in shape with only a few tending to the dumbbell-shaped type. No abaxial cuticular papillae were observed. Adaxial microhairs are similar to those of *P. colorata* in having longer distal cells than the basal cells (Figure 45a.3D).

This anatomical configuration certainly closely approaches that so characteristic of *P. colorata* and its close allies. However, *P. calcicola* var. *calcicola* is definitely not as close to *P. colorata* as are species like *P. alticola*, *P. tortuosa*, *P. malouinensis* and *P. elegans*. Nevertheless, the anatomy suggests that it is correctly placed together with this group of species in Group 3A.

Although the relationships of *P. calcicola* appear to lie with this group, the overall similarity in leaf anatomy between var. *calcicola* and *P. cirrhulosa* of Group 1B is very striking indeed. Only the mesophyll tissue differs slightly between these two taxa, with that of *P. cirrhulosa* being less compact than that of var. *calcicola* as a comparison of Figures 9.1 and 45a.1 shows. The mesophyll of *P. cirrhulosa* has been classified with the mesic type

characteristic of the glandular species of Group 1, whereas that of *P. calcicola* seems to have more in common with the sclerophyllous type characteristic of the eglandular species Groups 3–6. However, all other anatomical features of these two taxa, such as leaf outline, bundle arrangement, abaxial cell size, abaxial epidermal pattern, absence of stomata and microhair type, are very similar indeed and seem to imply a close affinity for these two taxa. They are separated into completely different species groups on the basis of the presence and absence of glands which may have been secondarily lost in *P. calcicola* (and even the *P. colorata* species group).

Only *P. cirrhulosa* specimens from the limestones of the De Hoop area, where they are sympatric with var. *calcicola*, were examined in this study. Additional material must be examined from other habitats before the significance or otherwise of the anatomical similarities between these two taxa can be evaluated. This is also necessary to appreciate the apparent correlation between the possession of glands and the mesic mesophyll type. With the information available at present it is only possible to speculate that the apparent similarities between these two taxa result from convergence in response to the edaphic habitat shared by all the specimens examined in this study.

SPECIMENS EXAMINED

CAPE.—3419 (Caledon): between Gansbaai and Hermanus, (–CB), *Ellis* 2511. 3420 (Bredasdorp): 24 km north of De Hoop turnoff on Arniston road, (–AD), *Ellis* 1282, Wydegelegen, *Ellis* 1666, 1667, 5148, De Hoop, *Ellis* 5447, 5448, 5449.

45b *P. calcicola* Linder var. *hirsuta* Linder pp. 260–262 (Linder & Ellis 1990a: 83)

This variety can be readily distinguished from var. *calcicola* by the consistent presence of numerous abaxial macrohairs. These hairs are soft and flexible, relatively short and are noticeably swollen towards the base (Figures 45b.2; 45b.3A, B). They are superficially inserted in the epidermis between one or two inflated epidermal cells (Figure 45b.2D) and are not associated with a raised cushion.

Structurally similar macrohairs occur on several glandular *Pentastichis* species of Group 1: *P. pallida* form F (Figure 7f.3E–H), *P. tomentella* (Figure 10.3), *P. airoides* (Figures 13a.2; 13b.2), *P. capillaris* (Figure 14.2), *P. oreodoxa* (Figure 23.3) and *P. setifolia* (Figure 24.2). In all these taxa the macrohairs are superficially inserted between a few inflated epidermal cells.

Except for the presence of these hairs, there are no anatomical differences between var. *hirsuta* and var. *calcicola*, and the discussion of the latter taxon is applicable to this taxon.

It may be significant that var. *calcicola* closely resembles *P. cirrhulosa* in leaf anatomy, suggesting a possible link to the glandular *Pentastichis* species of Group 1. This possibility is further strengthened by the macrohairs on var. *hirsuta* which resemble those of many Group 1 taxa

but are unknown in any of the eglandular groups. The affinities of *P. calcicola* are uncertain with the evidence being contradictory. However, this taxon should prove invaluable in gaining a better understanding of phylogenetic relationships within the genus.

SPECIMENS EXAMINED

CAPE.—3420 (Bredasdorp): 20 km north of De Hoop turnoff on Arniston road, (–AD), *Ellis* 2530, Wydegelegen, *Ellis* 5149, 5150, De Hoop, *Ellis* 5451. 3421 (Riversdale): 3 km E of Melkhoutfontein, (–AD), *Ellis* 1654.

46 *P. montana* Linder p. 263 (Linder & Ellis 1990a: 83)

A high altitude species of dry habitats which forms compact, low cushions, it is superficially similar to *P. pallida* except that it is glandless. It is poorly known and was insufficiently sampled for this study.

The distinctive anatomy of this species, with the unique continuous hypodermal sclerenchyma layer not linked by girders to the vascular bundles, supports the recognition of this taxon as a separate species. However, the anatomy does not support its position in Group 3 with *P. colorata* and its relatives. No anatomical features are shared between *P. montana* and the *P. colorata* species complex and its affinities do not appear to lie with this group.

The anatomy indicates that *P. montana* actually has mesic leaf anatomy and that it really belongs in Group 1 with the glandular species. The typical mesic structure has been highly modified in this taxon by xerophilic or cryophilic adaptations but the chlorenchyma can, nevertheless, be assigned to the mesic type. Similar modifications in high altitude plants of *P. pallida* form B are illustrated in Figure 7b.8 and serve to demonstrate the extent of modification possible in the mesic leaf type. These plants of *P. pallida* form B are also very short with hard rolled leaves and with a cushion-forming habit. However they are glandular in contrast to *P. montana* which lacks glands entirely but is superficially similar to *P. pallida*. The anatomy suggests that although *P. montana* appears to have lost all glands, it nevertheless belongs with the Group 1 species, possibly together with the anatomically specialized high altitude plants of *P. pallida* form B. Unfortunately very little material of either of these taxa was available for study and further collections are needed to gain a better understanding of the variation in these two taxa, which might provide additional clues as to their relationships.

SPECIMENS EXAMINED

CAPE.—3319 (Worcester): Gydoberg, Leeuwfontein Peak, (–AD), *Ellis* 2479; Keeromsberg, (–DA), Linder 4413.

47 *P. rigidissima* Pilg. ex Linder pp. 264–267 (Linder & Ellis 1990a: 85)

This species is widespread in the Cape mountains, from the Cederberg in the west to Cockscomb in the east. It is usually restricted to rock crevices in bedrock situations

at higher altitudes. It is variable in morphology with plants from more mesic mountains being soft to slightly prickly, whereas plants from the arid margins of the fynbos form large, extremely spinescent cushions. The variation is continuous with many intermediate forms and is reflected in the leaf anatomy illustrated in Figure 47.1.

Many anatomical features vary along this gradient: leaf size and number of vascular bundles, the nature of the adaxial channel, the degree of development of the abaxial girders and hypodermal layer as well as cell size and degree of compactness of the mesophyll tissue (Figures 47.1; 47.2). Epidermal structure is also variable along a similar gradient with zonation and microhairs evident in specimens without a continuous abaxial hypodermal layer (Figure 47.3A–C). These specimens have elongated, fusiform long cells with slightly sinuous walls and small, angular silica bodies, whereas the thick, spinescent leaves have short, rectangular long cells with pitted walls and circular silica bodies (Figure 47.3D–F).

This excessive variation makes anatomical diagnosis of *P. rigidissima* very difficult but it is, nevertheless, correlated with habitat. The smallest, softest leaves are associated with plants from the moister habitats from throughout the distribution range of *P. rigidissima* and the thicker, harder, more spiny leaves are only found on plants from the more arid northern aspect slopes. Although this degree of variation is greater than that normally encountered in the taxa of the eglandular *Pentstemon* species (Groups 3–6), a consistent basic structural arrangement is, nevertheless, evident throughout the large and representative sample studied. The anatomical data, therefore, supports the broad circumscription of this variable species.

A significant proportion of specimens is dubiously assigned to *P. rigidissima*, and some of these might be better placed in *P. colorata* as judged by the morphology. This is not supported by the leaf anatomy, however, as *P. rigidissima* and *P. colorata* differ considerably in leaf anatomy. Most of the diagnostic features of the *P. colorata* complex of species are not shared with *P. rigidissima*. Thus *P. rigidissima* does not have bigger intercostal abaxial long cells than the costal cells (although the abaxial epidermal cells are larger than the adaxial ones), the adaxial epidermis is not papillate, the silica bodies are not consistently dumbbell-shaped and the chlorenchyma is not typical of the sclerophyllous type, the cells being larger with a tendency to be more diffusely arranged.

All these features in combination suggest affinities with *P. exserta* (Figures 54.1–54.3) and *P. basutorum* (Figures 55.1; 55.2) of Group 3B which share a very similar leaf anatomy with *P. rigidissima*. These taxa in turn resemble *Merxmüllera disticha* and its allies (Ellis 1980a) rather closely in leaf anatomy. Whether this resemblance is phylogenetically meaningful is unknown but it may be significant because a similar link between *P. colorata* and its allies of Group 3A, as well as *P. tysonii*, *P. holciformis* and *P. praecox* of Group 3B, and *Merxmüllera stricta* was indicated by the leaf anatomy. *M. disticha* and *M. stricta* appear to represent two different evolutionary lines (Ellis 1981b), each linked to other *Merxmüllera* species, and possibly to several species of *Pentstemon* belonging to Groups 3A & B as well.

SPECIMENS EXAMINED

CAPE.—3219 (Wuppertal): Cederberg, Sneekop Peak, (–AC), Ellis 5518, Middelberg North Peak, Ellis 5585. 3318 (Cape Town): Table Mtn, (–CD), Esterhuysen 28058. 3319 (Worcester): Tulbagh, Groot Winterhoek Mts, (–AA), Esterhuysen 26999; Hex River Mts, Milner Peak, (–AD), Ellis 5531, 5534; Matroosberg, (–BD), Ellis 5812, 5813, 5974, Acocks 19088. 3320 (Montagu): Langeberg, Grootvadersbos, (–DD), Ellis 5548. 3321 (Ladismith): Groot Swartberg, Waboomsberg, (–BD), Ellis 5619, 5622, 5624, 5625; Towerkop, (–CA), Esterhuysen 26744. 3322 (Oudtshoorn): Swartberg Pass, (–AC), Ellis 2558, Acocks 18995. 3324 (Steytlerville): Groot Winterhoek Mts, Cockscomb Peak, (–DB), Ellis 5606, 5611, 5612. 3419 (Caledon): Riviersonderend Mts, Wa-en-Osse Peak, (–BA), Ellis 5562.

48 *P. malouinensis* (Steud.) Clayton pp. 268–270 (Linder & Ellis 1990a: 87)

P. malouinensis, like the awnless form of *P. alticola*, has blunt glumes without awns. These two taxa may, as a consequence, be confused but *P. malouinensis* always has glabrous leaves. It is very common in the southwestern Cape, occupying a wide range of mountain habitats.

This wide ecological tolerance is reflected in the very variable leaf anatomy, particularly the leaf in transverse section as illustrated in Figure 48.1. Leaf blades may be permanently inrolled, thick and setaceous with pronounced adaxial ribs and cleft-like furrows (Figure 48.1A–C) to more open and thinner without adaxial ribs (Figure 48.1D–G). These open leaf blades have larger bulliform cells and abaxial ribbing may even be developed (Figure 48.1G).

The anatomical structure of all these leaf blade types is remarkably constant despite this variability in leaf blade outline. The mesophyll is compact with small isodiametric cells, first and third order bundles alternate across the leaf width, and the abaxial epidermal cells are considerably larger than those on the adaxial surface. *P. malouinensis* shares all these features with the *P. colorata* complex and undoubtedly is correctly placed here in Group 3A notwithstanding the complete absence of awns.

The epidermal anatomy also supports this relationship of *P. malouinensis*. Epidermal zonation is clearly developed, the silica bodies are consistently dumbbell-shaped, the intercostal long cells are rather short and fusiform with sinuous walls, abaxial stomata are completely absent and microhairs occur (Figure 48.2). These microhairs have longer distal cells than the rather inflated basal cell (Figure 48.3B). The adaxial epidermal cells are somewhat inflated, although not to the same degree as in *P. colorata*. All these features are also consistent with those diagnostic for the *P. colorata* complex although no abaxial cuticular papillae were observed on *P. malouinensis*.

P. malouinensis, therefore, conforms very closely with all the species of the *P. colorata* complex. Close affinities are suggested by the leaf anatomy between all these taxa and they form a homogeneous anatomical assemblage.

SPECIMENS EXAMINED

CAPE.—3219 (Wuppertal): Cederberg, Algeria Forest Reserve, (–AC), Ellis 5583. 3318 (Cape Town): Jonkershoek State Forest, (–DD), Ellis

2248. 3319 (Worcester): Groot Winterhoek, Groen Mtn, (-CC), *Ellis* 5503; Keeromsberg, Tierhoek, (-DA), *Linder* 4432. 3320 (Montagu): Langeberg, Tradou Pass, (-DC), *Ellis* 5153, 5542. 3321 (Ladismith): Langeberg, Garcia's Pass, (-CD), *Ellis* 2538. 3322 (Oudtshoorn): George Dist., Montagu Pass, (-CD), *Ellis* 5826. 3324 (Humansdorp): Kareedouw Pass, (-CD), *Ellis* 5832; Groot Winterhoek Mts, Cockscomb Peak, (-DB), *Ellis* 5613. 3418 (Simonstown): Cape of Good Hope Nature Reserve, (-AB), *Ellis* 2859; Kogelberg, (-BD), *Ellis* 2345, 2346, *Boucher* 1729.

49 *P. pusilla* (Nees) Linder

pp. 271, 272 (*Linder & Ellis* 1990a: 89)

This species has recently been transferred to *Pentastichis* from *Poaegrostis*. It appears to be a specialized species of *Pentastichis* in which the florets are reduced to one. It is highly variable and appears to contain two taxa which can be distinguished on morphological and anatomical grounds.

The first forms tangled mats and has expanded leaves. The leaf anatomy is illustrated in Figure 49.1A–D. The leaves are exceptionally thin, with mesic mesophyll, small, widely spaced vascular bundles and with large epidermal cells (Figure 49.1A, C). The epidermis has very large fusiform long cells; no, or very few, stomata; microhairs with very short basal cells may be present; the costal silica bodies are dumbbell-shaped, but a large proportion may be nodular (Figures 49.1B, D; 49.2).

The second form of *P. pusilla* has erect culms and rolled leaves (Figure 49.1E, F). Its anatomy resembles that of *P. colorata* and its allies very closely. Features such as the abaxial papillae, large abaxial intercostal long cells, the silica bodies and microhairs suggest affinities with the *P. colorata* complex. This resemblance is so strong that it suggests that these specimens of *P. pusilla* are in fact awnless specimens of *P. alticola* which, in addition to the awns, have also lost a spikelet from each floret. The awnless specimens of *P. alticola* are unusual in having cushion-based macrohairs (Figure 43.2), a feature shared with this form of *P. pusilla* (Figure 49.1E). In the remainder of this discussion it will be assumed that these specimens should be treated with *P. alticola* and that *P. pusilla* comprises only those specimens discussed under form one above.

The specimens of *P. pusilla* with expanded, thin leaves have unusual anatomy for an eglandular species of *Pentastichis*. The mesic nature of the mesophyll, the thin expanded blade, the absence of sclerenchyma girders, the large intercostal zones and the dumbbell silica bodies all suggest affinities with the glandular species of Group 1 and not the eglandular Group 3 species with their sclerophyllous type of leaf anatomy. In all these respects *P. pusilla* is anomalous and its placing in the *P. colorata* complex of species is not supported by the leaf anatomy. However, the leaf anatomy also does not suggest close ties for this species and it should perhaps be left ungrouped at present.

If *P. pusilla* is correctly aligned with *P. colorata*, the mesic type of anatomy implies that it is, in fact, an extreme modification of the sclerophyllous type. There are no other taxa in which a similar derivation of the mesic type is

suggested. In the *Pentastichis* species with mesic mesophyll, modification has occurred which closely approaches that of the sclerophyllous type but the reverse is not known, with the possible exception of *P. pusilla*. Additional studies on this unusual species are required to reveal its true relationships.

SPECIMENS EXAMINED

CAPE.—3219 (Wuppertal): Cederberg, Algeria, (-AC), *Ellis* 5590. 3318 (Cape Town): Table Mtn, (-CD), *Linder* 4668. 3319 (Worcester): Witzenberg Mts, (-AC), *Ellis* 2481; Du Toitskloof Pass, Suurvlakte, (-CA), *Esterhuysen* 22775.

50 *P. elegans* (Nees) Stapf

pp. 273, 274 (*Linder & Ellis* 1990a: 90)

This is an exceedingly rare species which is poorly understood morphologically. The relationships of *P. elegans* are also uncertain. A single population of *P. elegans* from Viljoenshof in the Bredasdorp District was located for the anatomical study. This small population was growing in unploughed remnants of Coastal Fynbos in grey, clayey sand overlying an impervious layer.

The anatomy of these specimens confirms the grouping of *P. elegans* in Group 3A together with the *P. colorata* complex. It possesses most of the anatomical character set which is characteristic of *P. colorata* and its close allies. The mesophyll is typically compact (Figure 50.1B), the abaxial intercostal long cells are larger than the adaxial ones (although adaxial bulliform cells mask this size difference) (Figure 50.1A, B), silica bodies are dumbbell-shaped (Figure 50.1D), abaxial stomata are absent (Figure 50.1C, D) and the adaxial long cells are inflated and overarch the stomata (Figure 50.2D).

P. elegans also differs from *P. colorata* in several features such as the well-developed adaxial bulliform cells, the apparent complete absence of microhairs, the very prominent macrohairs and the absence of abaxial cuticular papillae. The open nature of the leaf blade is also distinctive. However, identical cushion-based macrohairs are common on the awnless form of *P. alticola* (Figure 43.2A, C) and a specimen of *P. colorata* (*Ellis* 5993), also from the Bredasdorp District at Waterford, has an identical leaf outline as well as marginal macrohairs of identical structure. Thus none of these characteristic features of *P. elegans* is unique to this species but all occur elsewhere in this closely related complex of species. The relationships of *P. elegans* are clearly with *P. colorata* and its allies of Group 3A.

SPECIMENS EXAMINED

CAPE.—3419 (Caledon): Bredasdorp Dist., Viljoenshof on road to Dirkuyskraal, (-CA), *Ellis* 5982, 5983.

Group 3B

The leaf anatomy of this group is heterogeneous with two groupings of taxa evident, each with a different anatomical configuration. Although all Group 3B taxa have

permanently infolded, setaceous leaves, these two groups are distinguished mainly by chlorenchyma differences. Several taxa have chlorenchyma tissue of small, isodiametric cells with centrally located vacuoles—typical of the sclerophyllous type, whereas the mesophyll tissue in others tends to consist of larger cells (also often with angular walls) but with vacuoles often not discernible. These cells may be rather loosely arranged with intercellular air spaces visible, particularly at the bases of the adaxial furrows. This tissue may represent a xerophilic or cryophilic adaptation of the mesic anatomical type even though the leaf outline and sclerenchyma distribution is typical of the sclerophyllous leaf type.

P. tysonii, *P. holciformis* and *P. praecox* of Group 3B have the typically sclerophyllous mesophyll whereas *P. chippindalliae*, *P. exserta* and *P. basutorum* have the modified mesic type of chlorenchyma. Each of these groups of species shows similarities with some species in Group 3A as judged by the mesophyll tissue in combination with a suite of other anatomical features.

The *P. colorata* species group of Group 3A (*P. colorata*, *P. tortuosa*, *P. alticola*, *P. calcicola*, *P. malouinensis* and *P. elegans*) shares many anatomical features, in addition to the sclerophyllous mesophyll, with *P. tysonii*, *P. holciformis* and *P. praecox* of Group 3B. Important characters in this regard are the papillate adaxial epidermis, the abaxial epidermal cells being larger than the adaxial ones and a tendency to dumbbell-shaped silica bodies.

All these taxa share these features with *Merxmuellera stricta* and its allies (Ellis 1980b, 1981b). The Group 3B taxa with this type of anatomy are anatomically very similar indeed to *M. stricta* as illustrations of *P. tysonii* in Ellis (1980b: figures 29–32) clearly show. From this comparison it is clear that *P. tysonii* (and *P. holciformis* and *P. praecox*) compare particularly closely to the Cathedral Peak and Drakensberg forms of *M. stricta*, both of which also have dumbbell-shaped silica bodies.

P. tysonii, *P. holciformis* and *P. praecox* actually resemble these forms of *M. stricta* more closely than they do any taxa in the *P. colorata* complex of Group 3A. They appear to be true intermediates linking the *P. colorata* complex with *M. stricta* and its allies. This relationship is not reflected in the current taxonomy and implies a need for generic realignment in the Arundinoideae.

The other Group 3B species (*P. chippindalliae*, *P. exserta* and *P. basutorum*) also show anatomical similarities with taxa of Group 3A, but not with the *P. colorata* complex. These taxa resemble *P. rigidissima*, and to a lesser extent, *P. montana*. Apart from the mesophyll tissue, which is not as compact as is usual for the sclerophyllous anatomical type, this group of species differs from the *P. colorata*–*P. tysonii*–*Merxmuellera stricta* alliance in several other anatomical attributes. The adaxial epidermal cells are not papillate or inflated and the abaxial epidermal cells are not larger than the adaxial ones. Silica bodies in this group of species are not dumbbell-shaped.

The sequence of arrangement of the different orders of vascular bundles across the blade width is another feature

which unites this group of species and serves to separate them from the *P. colorata*–*P. tysonii*–*Merxmuellera stricta* group. In these latter taxa lateral first order bundles are not separated by smaller vascular bundles whereas in *P. exserta*, *P. chippindalliae* and *P. basutorum* (as well as usually in *P. rigidissima*), first and third order vascular bundles alternate across the leaf blade. A similar difference in vascular bundle sequence also serves to separate *Merxmuellera stricta*, *M. guillarmodiae*, *M. stereophylla* and *M. drakensbergensis* from *M. disticha* and its allies such as *M. davyi* and *M. macowanii* (Ellis 1981b). It, therefore, seems as if a link exists between *P. exserta* and the other eglandular species of *Pentastichis* which do not have typical compact mesophyll, and *Merxmuellera disticha* and its allies (Ellis 1980a). This contrasts with the link suggested between the taxa of Groups 3A and 3B with compact mesophyll and *Merxmuellera stricta* and its allies.

Thus the taxa of Group 3B display anatomical links with the two anatomical lines identified in Group 3A as well as the two major lines in *Merxmuellera*. Major changes in generic concepts will be necessary to reflect these anatomical indications in the taxonomy of all these taxa. Whether these taxonomic changes are fully justified will depend on a synthesis of the data with all other information. Nevertheless, the results strongly suggest a total realignment of the taxa of Groups 3A and 3B as well as the taxa belonging to both the *Merxmuellera stricta* and the *M. disticha* species groups.

51 *P. tysonii* Stapf

pp. 274–277 (Linder & Ellis 1990a: 90)

P. tysonii is a summer rainfall species of the Drakensberg Mountains from the eastern Cape Province to the northern Natal Drakensberg. Awn length is variable and Hilliard & Burt (1987) recognised several variants on this basis. However, this variation is continuous and is not sufficiently correlated with other variable characters to justify subdivision of the species.

The leaf anatomy is also rather variable as illustrated in Figure 51.1A, C, E, F. Characters which vary are the size of the abaxial epidermal cells, the degree of inflation of the adaxial papillae and whether the abaxial girders are fused or not. This anatomical trend tends to follow the morphological trend of decreasing awn length, but this congruence is not perfect in that several specimens with long awns have anatomy similar to that of Figure 51.1G e.g. *Ellis 1409* (Figure 51.1H). This confirms that the variation is continuous and not correlated with morphology or distribution and supports the decision not to subdivide the species.

Despite this anatomical variability, a basic structural pattern is evident throughout the sample studied. These features are also evident in the illustrations of Robbertse (1959). Consistent characters are the very deep adaxial furrows on either side of the median vascular bundle, lateral ribs and furrows are absent or only slightly developed and the sequence of different orders of vascular bundle are the same. A small third order bundle is present on either side of the median bundle and this is followed

by 2–4 successive first order bundles. These are not interspaced by third order bundles but smaller bundles do occur in association with the margin.

This distinctive combination of characters is shared with *P. holciformis* and *P. praecox* (both also of Group 3B) as well as *P. colorata* and its allies of Group 3A. In addition this structural pattern is identical to that of *Merxmuellera stricta* (Ellis 1980b), particularly the Drakensberg form (*M. guillarmodiae*) of this species. All the anatomical forms of *P. tysonii* are illustrated in Ellis (1980b) as *P. tysonii* and *Pentastichis* sp. The Drakensberg form of *M. stricta* also has abaxial microhairs and dumbbell-shaped silica bodies but differs from *P. tysonii* in having abaxial stomata. The anatomy suggests a very strong relationship between all these taxa.

The inflated papillae on the adaxial epidermal cells of *P. tysonii* (Figure 51.3C, D) and all the other associated taxa serve to distinguish them from all other species of *Pentastichis* as well as the *Merxmuellera disticha* group of species, *Pentameris* and *Pseudopentameris*. The anatomy indicates that it may be preferable to recognize all these taxa as a separate genus in which three subgeneric groupings would be apparent. These would include the *P. colorata* complex and the *Merxmuellera stricta* complex, with *P. tysonii*, *P. holciformis* and *P. praecox* intermediate.

The adaxial microhairs of *P. tysonii* are worthy of comment as the distal cell is very small in relation to the length of the basal cell (Figure 51.3F and Robbertse 1959). This structure differs considerably from that of *P. colorata* (Figures 41.5D, H; 41.6D), *P. tortuosa* (Figure 42.3D), *P. alticola* (Figure 43.1F), *P. calcicola* (Figures 45a.3D; 45b.3D) and *P. malouinensis* (Figure 48.3E, F) of Group 3A, in which the basal cell tends to be only slightly longer than the distal cell or may even be shorter. Adaxial microhairs do not appear to occur on *Merxmuellera stricta* although the Drakensberg form of this species was not examined under the SEM. This observation suggests that the *P. colorata* group of species should be recognised as a subgroup of the group to which *P. tysonii* and its allies belong.

SPECIMENS EXAMINED

O.F.S.—2828 (Bethlehem): Drakenberg Mts, Mont-aux-Sources, Sentinel Peak, (–AB), Ellis 5725.

NATAL.—2929 (Underberg): Drakensberg Mts, Cathedral Peak, Organ Pipes Pass, (–AA), Ellis 3291, 3292, 3296, 3312, 5715, Killick 2280; Giants Castle Game Reserve, Bannermans Hut, (–AD), Ellis 3314, 3319, 3320; Cathedral Peak, Windy Gap, (–DA), Ellis 1409.

52 *P. holciformis* (Nees) Linder

pp. 278, 279 (Linder & Ellis 1990a: 91)

This species is a winter rainfall member of the *P. colorata*–*P. tysonii*–*Merxmuellera stricta* alliance. It occurs in the mountains between Paarl and the Bot River and is unusual in flowering as late as March. This may indicate a link to the summer rainfall species as growth is limited to the warmer, although drier, summer months. All the other taxa of Group 3B are summer rainfall species

and the morphology, as well as the leaf anatomy, support affinities between *P. holciformis* and these other Group 3B taxa. Close affinities between summer rainfall and winter rainfall species of *Pentastichis* are very rare, particularly amongst the eglandular taxa, and *P. holciformis* is unusual in this regard.

The leaf anatomy of *P. holciformis* is very similar indeed to that of *P. tysonii*. All the distinctive anatomical features of *P. tysonii* are also present on *P. holciformis* which has the same leaf outline, the same adaxial furrows on either side of the median bundle and the same pattern of arrangement of the vascular bundles as a comparison of Figures 51.1 and 52.1 clearly shows. The abaxial epidermal cells are also consistently larger than the inflated adaxial cells, a feature also evident on *P. tysonii*. No abaxial stomata are present. Dumbbell-shaped silica bodies do not occur on *P. holciformis* as is also the case on many *P. tysonii* specimens.

Leaf anatomy clearly supports a close relationship between *P. holciformis* and *P. tysonii* as well as *P. praecox*. *P. holciformis* most closely resembles those specimens of *P. tysonii* which are most similar to *Merxmuellera stricta* in leaf anatomy (Figure 51.1E–H) whereas *P. praecox* resembles the remainder of the *P. tysonii* specimens (Figure 51.1A–D). *P. tysonii*, therefore, appears to be intermediate between these two closely related taxa of Group 3B and seems to form a link between these species and the *P. colorata* complex, as well as with *Merxmuellera stricta* (particularly the Drakensberg form).

SPECIMENS EXAMINED

CAPE.—3418 (Caledon): Grabouw, Steenbras Dam, (–BB), Linder 4866.

53 *P. chippindalliae* Linder

pp. 280–282 (Linder & Ellis 1990a: 92)

P. chippindalliae is a summer rainfall species. It is a Transvaal endemic, occurring in the eastern Transvaal Drakensberg and Steenkampsberg on quartzitic soils. This newly described species has proved to be exceptionally difficult to study anatomically as both transverse sections and epidermal scrapes were generally unsatisfactory. This is unusual in the setaceous-leaved *Pentastichis* species where, even although the leaves are tough and wiry, good quality sections were relatively easy to obtain.

All the diagnostic anatomical features of *P. exserta* and its allies (*P. basutorum* and *P. rigidissima* in particular) are also present in *P. chippindalliae*. These include alternating first and third order vascular bundles with the third order bundles not associated with abaxial girders, in addition to the mesic type of mesophyll. The chlorenchyma tissue in *P. chippindalliae* is particularly diffuse with irregularly arranged cells interspaced with numerous intercellular air spaces (Figure 53.1). This mesophyll can definitely not be accommodated in the sclerophyllous type although the leaf outline is typically setaceous and displays many xeromorphic features.

Relationships of *P. chippindalliae* appear to lie with *P. exserta* and its allies as discussed under *P. exserta*. It does not belong to the group of species associated with *P. tysonii*.

Despite basic similarities with *P. exserta*, *P. chippindalliae* can easily be distinguished from related species by several anatomical features. The prominent adaxial ribs and furrows (Figure 53.1) do not occur in other species of this alliance except *P. rigidissima* (Figure 47.2). Abaxial macrohairs (Figure 53.2) only occur on this species although they appear to be readily deciduous but the associated basal cells are then visible (Figure 53.3D). Adaxial macrohairs may also be common (Figure 53.2D), a feature shared with *P. basutorum*. Abaxial microhairs do not occur on *P. chippindalliae* and, when present on the adaxial surface, tend to be very irregular in shape and may even consist of three cells (Figure 53.2E). These features in combination, therefore, serve to distinguish *P. chippindalliae* from its close relatives.

SPECIMENS EXAMINED

TRANSVAAL.—2530 (Lydenburg): Dullstroom Dist., Steenkampsberg, Die Berg, (—AA), *Ellis* 3447, 3451, 4451, 4452; Lydenburg Dist., Long Tom Pass, (—CA), *Ellis* 5734.

54 *P. exserta* Linder

pp. 282–285 (Linder & Ellis 1990a: 92)

P. exserta is a summer rainfall species of the Natal Drakensberg where it is found in grassland communities, often in association with *P. tysonii*. Morphologically it can easily be confused with *P. tysonii* but the nature of the lateral awns serve to distinguish these two species.

Although *P. exserta* and *P. tysonii* are morphologically very similar, their leaf anatomy differs considerably and they can easily be distinguished on this basis. In fact, the anatomy suggests that these two species are not particularly closely related and that they should be accommodated in different species groups.

P. exserta can be distinguished by the alternating first and third order vascular bundles. The smaller bundles are not associated with sclerenchyma girders, particularly on the abaxial side (Figure 54.1D, H, I). The less compact mesophyll, often with air spaces visible and with rounded cells as seen in transverse section (Figure 54.1) also serves to distinguish *P. exserta* from *P. tysonii* and its allies. The abaxial epidermis of these two species is very similar but the adaxial epidermis differs in that inflated papillae do not occur on *P. exserta* (Figure 54.3D) but are always present on *P. tysonii* (Figure 51.3C, D).

All these features which serve to distinguish *P. exserta* from the morphologically similar *P. tysonii* are shared with *P. basutorum* (Figures 55.1; 55.2) and *P. chippindalliae* (Figures 53.1–53.3), also of Group 3B, as well as with *P. rigidissima* (Figures 47.1–47.4) and *P. montana* (Figure 46.1) of Group 3A.

All these taxa in turn resemble *Merxmuellera disticha* and its allies (Ellis 1980a) in this particular leaf anatomy.

Close affinities with *P. tysonii* and its relatives in Group 3B (*P. holciformis* and *P. praecox*), as well as with the *P. colorata* group of species of Group 3A, and *Merxmuellera stricta* and its allies, are not supported by the anatomical evidence. Instead, *P. exserta* shares similar anatomical features with a group of species, all of which do not have the classical sclerophyllous mesophyll type.

None of the species which resemble *P. exserta* in anatomy has glands but, nevertheless, they all do resemble some glandular species in these features of their leaf anatomy. Examples are the high altitude plants of *P. pallida* form B of (Figure 7b.8), *P. cirrhulosa* (Figures 9.1–9.3) and *P. lima* (Figures 11.1–11.3), all of Group 1B. This entire group of species shares alternating vascular bundles, non papillate adaxial epidermal cells, silica bodies not consistently dumbbell-shaped, in addition to the anomalous type of mesophyll tissue.

These observations suggest that glands have been lost in *P. exserta* and its allies of Group 3 and that these species should perhaps be associated with the glandular species mentioned above in a separate species group intermediate between the glandular and the eglandular groups. If distribution patterns of other non-anatomical characters support this arrangement it will strengthen the apparent correlation between presence of glands and the mesic type. At present it is very difficult to assign species with modified chlorenchyma to either the sclerophyllous or the mesic types with any degree of certainty. An unambiguous definition of these two basic leaf types will only be possible once all characters have been synthesised. The resultant groupings will indicate the exact nature of these two types and the maximum degree of modification that has occurred in nature.

SPECIMENS EXAMINED

O.F.S.—2828 (Bethlehem): Drakensberg Mts, Moni-aux-Sources, Sentinel Peak, (—DB), *Ellis* 5726, *Du Toit* 646.

NATAL.—2929 (Underberg): Drakensberg Mts, Cathedral Peak, Organ Pipes Pass, (—AA), *Ellis* 3300, 5723, 5724; Highmoor State Forest, (—BC), *Ellis* 3169, 5713, 5714; Sani Pass (—CB), *Du Toit* 2301; Garden Castle Forest Reserve, (—CC), *Ellis* 5700.

TRANSKEI.—3028 (Matatiele): Qacha's Nek Pass, (—BA), *Ellis* 5696; Naudesnek Pass, (—CA), *Ellis* 5687, 5688.

55 *P. basutorum* Stapf

pp. 286, 287 (Linder & Ellis 1990a: 94)

P. basutorum is also a summer rainfall species but is restricted to the Maluti Mountains to the west of the Drakensberg. It occurs in shallow soils overlying Cave Sandstone rock and has a very xeromorphic leaf anatomy.

The anatomy of *P. basutorum* is very distinctive due to the well-developed continuous, abaxial hypodermal layer. The first order vascular bundles are linked to this hypodermis by conspicuous girders which extend to slight adaxial ribs (Figure 55.1A, B). The third order bundles, however, are usually not associated with sclerenchyma girders or strands. The first order vascular bundles alternate with small third order bundles across the leaf width (Figure 55.1). A unique feature of *P. basutorum* is the

dense indumentum on the adaxial surface, the sectioned hairs being clearly visible in all sections (Figure 55.1). All these features are clearly illustrated in Robbertse (1959) and in Ellis (1980b).

The alternating bundles, in addition to the diffuse mesophyll tissue of small rounded cells with conspicuous intercellular air spaces (Figure 55.1D), clearly relate this species to *P. exserta* and its allies, *P. rigidissima* in particular. Similarities with *P. chippindalliae* and *P. montana* are not so close but a similar, basic leaf architecture is, nevertheless, evident.

All these eglandular species share similar anatomical features which suggests that they belong in a single subgeneric group apart from *P. tysonii* and its relatives. *Merxmuellera disticha*, particularly the typical form, is surprisingly similar to *P. basutorum* in leaf anatomy. Shared attributes are the hypodermis, alternating large and small bundles with the small bundles not connected to sclerenchyma girders and the cork-silica cell pairs with the elliptical silica body enfolded in a crescentic cork cell (Figure 55.2). Long adaxial pappillae also occur on this form of *M. disticha* and the indumentum on *P. basutorum* is probably formed by similar, but more elongated, pappillae which occur on *M. macowanii* (Ellis 1981b).

P. basutorum and these eglandular species sharing a basically similar leaf anatomy, also resemble some glandular species of *Pentaschistis* very closely. This possible relationship is discussed further under *P. exserta*.

SPECIMENS EXAMINED

O.F.S.—2828 (Bethlehem): Golden Gate Highlands National Park, Brandwag Peak, (—DA), Ellis 2367, 2368, 2369, 2370, 2373, Liebenberg 7454.

56 *P. praecox* Linder

p. 288 (Linder & Ellis 1990a: 95)

This summer rainfall species, which is closely allied to *P. tysonii*, is unusual in flowering in the winter and early spring, a feature it shares with *Merxmuellera aureocephala*. It occurs in the Natal Drakensberg from Bushmans Nek as far north as Royal Natal National Park.

The leaf anatomy clearly relates this species to *P. tysonii*, particularly to those specimens illustrated in Figure 51.1A–D. These differ somewhat in leaf blade outline from the remainder of the *P. tysonii* sample (Figure 51.1E–H) which in turn closely approximate the Drakensberg form of *Merxmuellera stricta* (Ellis 1980b). Thus irregular dumbbell-shaped silica bodies may occur on *P. praecox* (Figure 56.1B, C) as well as on some specimens of *P. tysonii*.

The basic leaf anatomy of *P. praecox* is identical to that described for *P. tysonii* and *P. holciformis* and these three taxa appear to be very closely related indeed. Although *P. praecox* is linked to *P. basutorum* by a similar inflorescence type, the leaf anatomy does not support a close relationship for these two species.

SPECIMENS EXAMINED

NATAL.—2929 (Underberg): Cobham State Forest, (—CB), Manning, Hilliard & Burt 15939; Loteni River, (—DA), Wright 461.

Group 4

This group includes eglandular *Pentaschistis* species often with cauline leaves which are expanded but thick and leathery. Anatomically it is a very homogeneous group and all taxa possess typically sclerophyllous mesophyll of small, compact cells with minute intercellular air spaces, despite the fact that the leaves are not permanently inrolled, as is more usual for the sclerophyllous leaf type. Typically all species assigned to this group have laminae which are thicker in the lateral parts close to the margin. The median vascular bundle is thus located in the thinnest part of the blade. This very striking feature is diagnostic for Group 4.

In addition, a number of anatomical features serve to characterize this very distinct group. Flat-topped adaxial ribs and cleft-like furrows occur throughout and first and third order vascular bundles alternate across the leaf width. The abaxial epidermal cells are uniform in size across the leaf width (although they often are larger laterally where the blade is thickest) and they are noticeably larger than the adaxial epidermal cells. Epidermal cell size does not vary between costal and intercostal zones.

Epidermal zonation is not present, and the long cells in a file alternate with cork-silica cell pairs, in which both cells are tall and narrow, or the silica cell may be elliptical. No abaxial stomata are present and abaxial microhairs are extremely rare, only being present on *P. caulescens*. The adaxial microhairs are extremely long and finger-like with a minute distal cell. The adaxial ribs characteristically are covered in prickly hairs which tend to interlock over the cleft-like furrows.

All taxa included in Group 4 by Linder & Ellis (1990a) conform to this anatomical diagnosis and are clearly separable from all other species of *Pentaschistis*. A possible exception is *P. pyrophila* of Group 3A and possibly *P. eriostoma* of Group 6. These two species tend toward the *P. curvifolia* group of species in leaf anatomy but do not have the thickened leaf margins. They both have the same type of elongated adaxial microhair with minute distal cells as do the species of Group 4. However, the adaxial prickles are particularly numerous and are much longer than those of Group 4—so much so that they can be regarded as macrohairs.

This adaxial epidermal structure closely resembles that of some species of *Pentameris*, such as *P. longiglumis* (Ellis 1985b), *P. macrocalycina* and *P. obtusifolia* (Ellis 1985d). These two *Pentaschistis* species, therefore, appear to provide a link between the Group 4 *Pentaschistis* species and these *Pentameris* species. This suggests that the relationships of all the Group 4 taxa should be sought with *Pentameris* and its allies rather than with any other species group in *Pentaschistis*.

The anatomy indicates, therefore, that this entire group of species should be accommodated together in a single supraspecific group. This implies that the present separation of *Pentastichis* and *Pentameris*, based on the presence or absence of a terminal tuft of bristles on the ovary, does not reflect phylogeny. Further taxonomic studies are needed to establish whether additional character correlations occur which support the anatomical indications.

Despite these intermediate species indicating a link with *Pentameris*, the leaf anatomy does not support a realignment of this species group. These peripheral species seem to be better accommodated together with *Pentameris macrocalycina* and its allies in a separate group close to Group 4. If this arrangement is followed the implications are that the affinities of the Group 4 species are closer to these *Pentameris* species than they are to any of the other *Pentastichis* species groups.

57 *P. curvifolia* (Schrad.) Stapf pp. 288–291 (Linder & Ellis 1990a: 96)

A widespread and common species of the fynbos vegetation, from Calvinia in the west to Grahamstown in the east, it is a distinctive species and can always be recognized by the contracted inflorescence and the thickened leaf margins. This latter diagnostic attribute reflects a unique anatomical feature of the leaf blades of *P. curvifolia* and its relatives. All specimens of *P. curvifolia*, from a very representative sample, have very conspicuous thickening of the leaf blade towards the leaf margin (Figure 57.1) and this very striking feature appears to be consistently present in this species. This lateral thickening is also illustrated by Robbertse (1959).

This lateral thickening results in a significant modification of the anatomical structure of the leaf margin. The alternating arrangement of first and third order vascular bundles may be disrupted in the thickened lateral parts of the blade and some small bundles may be absent (Figure 57.1H). The lateral third order bundles are also usually located at the bases of adaxial furrows rather than beneath ribs (Figure 57.1F–H). The massive ribs overlying the larger bundles may also be modified, tending to be flanged (Figure 57.1D, G, H). The first order bundles in this part of the leaf are associated with massive trapezoidal abaxial sclerenchyma girders which fuse laterally to form a continuous abaxial hypodermal layer (Figure 57.1F–H). The pattern in the epidermis overlying this thicker part of the blade is not altered but the width of the cells is much greater than those nearer the centre of the blade (Figure 57.2A, B).

This thickened leaf margin is diagnostic for all the taxa of Group 4 and *P. curvifolia* is undoubtedly the core species of this group. Despite its widespread distribution throughout the fynbos biome, as well as the wide range of habitats in which it is found (2 000 m to sea level), *P. curvifolia* displays surprisingly little anatomical variation as illustrated in Figures 57.1 and 57.2. Similarly the other segregate taxa of Group 4 are also very similar to *P. curvifolia* in leaf anatomy, *P. pungens*, *P. caulescens* and *P. scandens* in particular—this despite the fact that they

differ considerably in vegetative morphology from *P. curvifolia*. Only *P. acinosa* diverges somewhat from *P. curvifolia* but, nevertheless, retains the basic anatomical features of Group 4.

This anatomical consistency in the Group 4 taxa is in sharp contrast with *Pentastichis* in general. In most widespread species of this genus the degree of anatomical variation encountered is considerable, even in the eglan-dular species groups. A comparison of the anatomical variation present in *P. colorata* (Figures 41.1–41.4), another widespread species of diverse habitats, illustrates this point. In this species the intraspecific variation is as great as, or even greater, than that present between *P. colorata* and neighbouring taxa. *P. rigidissima*, also a widespread species but restricted to a specific habitat, also shows much more anatomical variation than *P. curvifolia*. See Figure 47.1 for transectional variation in this species.

Thus, although *P. curvifolia* is morphologically readily distinguishable from the other species of Group 4, this is not the case anatomically, due to the anatomical homogeneity of the group. *P. caulescens* and *P. scandens*, in particular, are virtually identical to *P. curvifolia* in leaf anatomy.

The adaxial prickles and slender, finger-like microhairs with minute distal cells (Figure 57.3), which are characteristic of *P. curvifolia* and the other Group 4 species, also suggest affinities with *P. pyrophila* (Figure 44.3) of Group 3A and *P. eriostoma* (Figure 68.4) of Group 7. Furthermore, this type of adaxial epidermal structure corresponds very closely to that of many species of *Pentameris*, and the relationships of *P. curvifolia* may lie with these taxa rather than with any other species group within *Pentastichis*.

SPECIMENS EXAMINED

CAPE.—3219 (Wuppertal): Koue Bokkeveld Mts, Citrusdal, (—CA), *Ellis* 2492; Groot Winterhoek Mts, Suurvlak Farm, (—CC), *Ellis* 5485. 3318 (Cape Town): Table Mtn, contour path above Kirstenbosch, (—CD), *Ellis* 2301, 2302, below Saddle, *Linder* 4336; Jonkershoek State Forest, Witbrug, (—DD), *Ellis* 2216, Jakkalsvlei, *Ellis* 2216, 2224, 2225, 2231, 2233. 3319 (Worcester): Franschhoek Pass, (—CC), *Ellis* 2351. 3320 (Montagu): Langeberg, Tradou Pass, (—DC), *Ellis* 646. 3324 (Steytlerville): Groot Winterhoek Mts, Cockscorn Peak, (—DB), *Ellis* 5610. 3325 (Port Elizabeth): Suurberg, Suurberg Pass, (—BC), *Ellis* 5837. 3418 (Simonstown): Cape Peninsula, Helderberg Plateau, (—AB), *Ellis* 2353, 2354; Cape Point Nature Reserve, (—AD), *Ellis* 2322, 2325; Cape Hangklip, (—BD), *Ellis* 2518. 3419 (Caledon): Hermanus, (—AD), *Ellis* 2513. 3422 (Mossel Bay): Mossel Bay, (—AA), *Ellis* 625.

58 *P. pungens* Linder pp. 292–294 (Linder & Ellis 1990a: 97)

This is a species of the western mountains of the fynbos biome, from the Cederberg to Tulbagh. Two ecotypes appear to exist, a montane form and specimens from lower altitudes in arid fynbos and these differ slightly in anatomy. In the moister mountains *P. pungens* is essentially a post-fire species which disappears from the vegetation three or four years after a burn. In the more arid habitats, where fire is a rare occurrence, *P. pungens* appears to be longer lived with narrower, more rigid leaves (Figure 58.1).

The leaf anatomy of *P. pungens* is very similar to that of *P. curvifolia* despite the fact that thickened margins are not so prominent in this species. The lateral parts of the blade are, nevertheless, usually thicker than the midlamina (Figure 58.1C, E). All other features of the transectional anatomy and epidermis correspond very closely to *P. curvifolia*. This applies particularly to the montane form. Specimens from the arid fynbos diverge the most and the margins may even be tapering (Figure 58.1A) and epidermal zonation may be evident (Figure 58.2A, B).

P. pungens undoubtedly belongs with *P. curvifolia* and its allies of Group 4. All anatomical indications support this classification. Shared characters are the thickening of the margin, the alternating vascular bundle arrangement, the brickwork long cell pattern, the adaxial prickles (Figure 58.3B, E) and distinctive microhairs (Figure 58.3C, F).

Despite being placed in the eglandular Group 4, sessile linear glands appear to be present on the margins of some specimens of *P. pungens*. Six to eight seriate glands may be visible in transection on a small marginal projection (Figure 58.1E, F). In surface view these are seen to be almost continuous along the entire leaf margin (Figure 58.2E, F). The constituent cells are very small and isodiametric.

This gland configuration and the constituent cells differ from those observed in all other *Pentastichis* species and it is not certain whether these structures do actually represent glandular tissue. Their location in a narrow, projecting margin is reminiscent of the Group 2B species such as *P. trisetata* (Figures 36.1, 36.2), *P. rosea* subsp. *purpurascens* (Figures 37b.1; 37b.2) and *P. pseudopallescens* (Figures 38.1), all of which share the same general distributional range with *P. pungens* and suggests that these structures do in fact represent sessile linear glands (Linder *et al.* 1990). The marginal glands of *P. trisetata* (Figure 36.2A), *P. rosea* subsp. *purpurascens* (Figure 37b.2F) and *Prionanthium dentatum* (Ellis 1989b) in surface view resemble those of *Pentastichis pungens* particularly closely in that they are multiserial and comprised of small isodiametric cells. These glands in all these other taxa are prominently nucleate, a feature not observed in *P. pungens*.

It would be unwise to attach too much importance to the occurrence of these gland-like structures in this eglandular group until it is established that these structures are indeed sessile glands. If this proves to be so, it will imply a drastic revision of species groups in *Pentastichis*. The placement of *P. pungens* in an eglandular species group is fully corroborated by all the other anatomical evidence.

If these structures do prove to be glands, *P. pungens* would then represent the only species with undoubted sclerophyllous anatomy in which glands occur. Apart from this possible exception, a perfect correlation exists between absence of glands and the sclerophyllous type of anatomy. Conversely the possession of glands and the mesic type are strongly correlated despite problems with the definition and recognition of mesic anatomy in highly modified leaf types.

Foliar glands in particular are often absent in taxa with the mesic type but their apparent presence in *P. pungens* seems to imply that they have also been secondarily lost in all the sclerophyllous taxa of Groups 3–6. Further study of *P. pungens* is required to resolve this basic question of relationships within the entire genus.

SPECIMENS EXAMINED

CAPE.—3219 (Wuppertal): Cederberg Mts, Algeria Forest Reserve, (–AC), Ellis 2506, Sneekop Peak, Ellis 5516, 5517, Middelberg North Peak, Ellis 5581, Helshoogte, Ellis 5791; Koue Bokkeveld Mts, 45 km from Citrusdal on road to Ceres, (–CD), Ellis 2488, 5122. 3319 (Worcester): Groot Winterhoek Wilderness Area, (–AA), Ellis 5795.

59 *P. acinosa* Stapf

pp. 295–297 (Linder & Ellis 1990a: 99)

This is an alpine species of the western and southern Cape, extending as far eastward as Riversdale. It is restricted to rock ledge habitats.

The anatomy of *P. acinosa* differs from that of *P. curvifolia* more than any other species in Group 4. Nevertheless, the basic anatomical structure of the leaf blade is such that it can still be accommodated comfortably in this group. The anatomical divergence of *P. acinosa* can possibly be explained by the very specialized habitat occupied by this species which may have necessitated anatomical adaptations. Similarities between *P. acinosa* and the rest of the Group 4 taxa are the thickening in relation to the leaf margin (Figure 59.1A–C) although this is not as obvious as in the other species of this group. The sequence of vascular bundles conforms to that of this group as does the additional abaxial sclerenchyma near the margin (Robbertse 1959). The abaxial epidermal long cells are consistently separated by pairs or groups of short cells and no microhairs or stomata are present on this surface. The finger-like adaxial microhairs with minute distal cells are typical of those of Group 4. All these features support affinities with the taxa of this group.

Despite these distinctive Group 4 features, *P. acinosa* has several features which differ from those of the group but the degree of difference does not appear to have taxonomic importance above the species level. The fusiform long cells (Figure 59.2C–F) and the abaxial costal zones (Figure 59.2A, C) differ slightly from the other taxa although both features can easily be derived from the character states present in the other species of this group. The zonation, in particular, is very indistinct and the costal silica bodies exceptionally variable in shape (Figure 59.2B, C). The absence of adaxial prickles with well-developed barbs is not consistent throughout the *P. acinosa* sample with some specimens with small adaxial prickle hairs (Figure 59.3E).

The most striking difference between *P. acinosa* and the other Group 4 taxa are the large adaxial epidermal cells (Figure 59.1B, D). These cells resemble bulliform cells in transection but in surface view are seen to be raised and inflated and overarch the stomata in the adaxial grooves (Figure 59.3B). They appear to interlock with sunken stomata on the opposite side of the cleft-like furrows and, under conditions of water stress may help

prevent transpiration by sealing the stomatal apertures. The presence of these inflated epidermal cells is particularly striking in surface view but similar cells are present in *P. curvifolia* as seen in transection (Figure 57.1E) but they are hidden in surface view by the interlocking prickles (Figure 57.3B, E). This difference, therefore, although visually striking, does not appear to be taxonomically important. All specimens of *P. acinosa* also do not have such inflated adaxial long cells (Figure 59.3E).

The classification of *P. acinosa* together with the Group 4 taxa is, therefore, not questioned by the anatomical evidence even although it diverges somewhat in leaf anatomy. Its relationships undoubtedly belong with *P. curvifolia* and its relatives.

SPECIMENS EXAMINED

CAPE.—3320 (Montagu): Langeberge, Grootvadersbos, (—DD), *Ellis* 5549, 5550. 3418 (Simonstown): Hottentots Holland Mts, Sugarloaf Peak, (—BB), *Ellis* 2267, 2268, 2278, Somerset Sneeukop, Landrostkop, *Ellis* 4678, 4681; Kogelberg, Platberg, (—BD), *Ellis* 2340. 3419 (Caledon): Riviersonderend Mts, Wa-en-Osse Peak, (—BA), *Ellis* 5560.

60 *P. caulescens* Linder

p. 298 (Linder & Ellis 1990a: 99)

A rare species found on shale bands and dry, stony slopes in the mountains of the south-western Cape Province, morphologically, *P. caulescens* appears to be an 'arid' derivative of *P. acinosa* but the anatomy indicates very close ties with *P. curvifolia*. From the leaf anatomy it appears as if *P. caulescens* is merely a xerophytic form of *P. curvifolia* but the morphological differences between these two species undoubtedly justify their separation.

The leaf anatomy of *P. caulescens* resembles that of *P. curvifolia* in virtually all respects. The leaves are much narrower, and often more tightly inrolled, than those of *P. curvifolia* but the basic anatomical structure is nevertheless identical. The classification of *P. caulescens* in Group 4 together with *P. curvifolia* is, therefore, fully supported by the leaf anatomy.

The only difference noted between *P. caulescens* and *P. curvifolia* is the occurrence of numerous abaxial microhairs on *P. caulescens* (Figure 60.1B, C). Despite the fully representative sample of *P. curvifolia* studied, abaxial microhairs were not seen on any specimen. As only a single specimen of *P. caulescens* was studied, it is not certain whether abaxial microhairs is a consistent character separating these two species.

The structure of the microhairs on *P. caulescens* may be informative as they are relatively short and wide with the tapering distal cell about equal in size to the basal cell. This is in marked contrast to the adaxial microhairs of all Group 4 taxa where these hairs are long and slender with minute distal cells. Unfortunately SEM studies were not possible on the adaxial surface of *P. caulescens* so the structure of its adaxial microhairs remains unknown. However, the structural differences between the abaxial and adaxial microhairs in this Group is considerable, much greater than has been reported for other grasses. Micro-

hair type is generally considered to be taxonomically meaningful in the Poaceae (Metcalf 1960) but the occurrence of two structurally very different types in the species of *Pentaschistis* Group 4, and perhaps even on *P. caulescens*, suggests that studies of both epidermides are needed before microhair structure in the Poaceae can be reliably described.

SPECIMENS EXAMINED

CAPE.—3319 (Worcester): Witzenberg Mts, Ceres Dam, (—AC), *Ellis* 2482.

61 *P. scandens* Linder

pp. 299–301 (Linder & Ellis 1990a: 101)

This species has a restricted distribution in the Bredasdorp District. It is confined to sandy soils along the coastal forelands.

The morphology indicates that this species is also a derivative of *P. acinosa*, as was the case with *P. caulescens*. However, the leaf anatomy points to very close links with *P. curvifolia*. In all respects the leaf anatomy of *P. scandens* resembles that of *P. curvifolia* and these two species cannot be distinguished on anatomical criteria. The growth forms of the two species are entirely different, however, and their specific status is not questioned by this anatomical resemblance. *P. scandens*, *P. curvifolia* and *P. caulescens* form an extremely tightly knit anatomical group with *P. pungens* and *P. acinosa* further removed. The leaf anatomy of *P. scandens* consequently supports the coherence of Group 4.

Features shared with *P. curvifolia* are the diagnostic thickened leaf margins, the alternating sequence of vascular bundle arrangement and the large abaxial epidermal cells. The absence of epidermal zonation, and the alternating sequence of rectangular long cells and cork-silica cell pairs is also distinctive. The abaxial epidermis has typical prickles tending to interlock over the cleft-like adaxial furrows as well as the slender, finger-like microhairs with minute distal cells which are so characteristic of Group 4 and its allies.

Thus, although this species is very rare and incompletely known, its affinities with the *P. curvifolia* species group are not questioned. The very unusual recurving of the old leaf blades, so typical of this species, surprisingly does not appear to be reflected in the leaf anatomy which is identical to that of *P. curvifolia* which has curly old leaf blades. It is possible that the thickened margins of all the Group 4 species cause stresses during the desiccation process which may account for the distinctive old leaves. Why their form should differ between species with identical anatomy is not apparent from this work.

SPECIMENS EXAMINED

CAPE.—3419 (Caledon): Bredasdorp Dist., Ratelrivier at base of Buffeljagsberg, (—CA), *Ellis* 5986, 5987, 5988.

Group 5

This is probably a heterogeneous group in which glands are absent, the leaves are expanded and leathery and the relatively small spikelets have the lemmas villous only at the base. In most species there is a reduction in the awns except in *P. capensis* which has long, soft awns.

An evaluation of the anatomy of this group was not possible as three of the four species occur only in Madagascar or mid-Indian Ocean islands and freshly fixed material was not available for study. Herbarium material was consequently used in this study but tissue reconstitution was such that accurate comparisons with South African taxa is not feasible. It was, therefore not possible to determine whether this group is also anatomically heterogeneous.

The only South African representative of this group is *P. capensis*. This species is unique in the genus in being a hydrophyte. In fact it is the only hydrophytic grass in the Cape Flora (Linder & Ellis 1990a) and shows considerable morphological and anatomical specialization to this habitat. As such it is difficult to compare with the other taxa in the group as it is not possible to determine which features are developed in response to this habitat or whether these features are characteristic of the group as a whole. This is compounded by the fact that the anatomical preparations of the other taxa are not of a similar standard, making comparative deductions unreliable.

It will only be possible to assess the homogeneity of this group when comparable material of the Madagascan species is studied. The present work will, therefore, be restricted to a discussion of the leaf anatomy of *P. capensis* in relation to the other South African species of the genus. Brief comments on the limited observations made on *P. andringitrensis* and *P. humbertii* will also be given. No material of *P. insularis* was examined and this species is not discussed in this paper.

62 *P. capensis* (Nees) Stapf

pp. 302–304 (Linder & Ellis 1990a: 103)

This species is unique in the genus, being a hydrophyte growing in fast-flowing mountain streams, often on the vertical faces of waterfalls. It is only found on sandstone substrates in the mountains of the south-western Cape Province from Riversdale to the Cape Peninsula and Tulbagh.

Morphologically *P. capensis* is very isolated in the genus with no obvious affinities with any other species. The central awns are unusual in that they lack twisted columns and are long and floppy.

Similarly, the leaf anatomy does not suggest close affinities with any other species in the genus. Several unique anatomical features are present which serve to distinguish *P. capensis* but do not provide clues as to the possible relationships of this interesting species.

The very prominent, globose, inflated papillae on the adaxial epidermal cells are unique in the genus and are clearly illustrated in Robbertse (1959). In transverse section they are clearly seen to occur on the adaxial ribs and on the sides of the steep furrows (Figure 62.1B–D) and the entire outer surface of the cell wall is seen to be convex, thin-walled and inflated. These constitute typical oblique papillae raised above the level of the stomata although they do not overarch them as is more usual. In surface view (Figure 62.3C) it can be seen that these papillae tend to interlock at the tops and sides of the adaxial furrows but they do not overarch the stomatal apertures (Figure 62.3D).

Located between the papillae are prickly hairs but the association between the papillae and these prickles is not as close as occurs in *Merxmuellera macowanii*, *M. davyi* (Ellis 1981b), *M. drakenbergensis* and *M. stereophylla* (Ellis 1981a). In all these species the adaxial prickly hairs are closely surrounded by 2–4 inflated papillae which appear to support the prickly hair and to hold it erect. It may be relevant to note that this feature is more developed on those specimens of these *Merxmuellera* species growing in moist situations than those from xerophytic lithophyte communities. In fact, these papillae were most evident on a specimen of *M. davyi* collected on a waterfall.

The presence of these papillae on *P. capensis* is, therefore, not a unique occurrence in the arundinoid grasses. They appear to confer an adaptive advantage to arundinoid grasses growing in fast-flowing water habitats but are not indicative of affinity as no other anatomical features are shared by *P. capensis* and these *Merxmuellera* species.

The chlorenchyma of *P. capensis* approaches the sclerophyllous type very closely with the angular cells compactly arranged (Figure 62.1B–D). The intercellular air space system is also very reduced as seen in transverse section, small air spaces only being visible immediately below the stomatal apertures. The individual chlorenchyma cells are slightly larger than is usual in the *Pentastichis* species with the sclerophyllous type of anatomy but this should not affect the placement of this species in this anatomical type. This compact mesophyll without well-developed air spaces or lacunae is very unusual in a hydrophyte and suggests that *P. capensis* may be adapted to survive periods of desiccation when stream levels are low.

The broadly expanded leaf of *P. capensis* is unusual amongst the sclerophyllous species but other exceptions are known, such as *P. tortuosa* (Figure 42.1) of Group 3A and *P. curvifolia* (Figure 57.1) of Group 4. Although most species with the sclerophyllous type have permanently infolded leaf blades, this correlation is not perfect. The absence of abaxial stomata also supports this view (Figure 62.2) as most species with sclerophyllous anatomy lack abaxial stomata.

The bundle sheath extensions in *P. capensis* are very conspicuous (Figure 62.1B–D). In fact *P. capensis* is the only member of the genus in which typical, thin-walled parenchyma extension cells occur. The sclerenchyma strands are also unusual in that the fibres are only slightly thickened. This feature resembles the condition in *Merxmuellera cincta* (Ellis 1982a) and *Pentameris obtusifolia*

(Ellis 1985d) but no other anatomical features of these two species suggest affinities with *P. capensis*.

The abaxial and adaxial microhairs of *P. capensis* (Figures 62.2B; 62.3A) deserve some comment. The abaxial hairs with the basal cell shorter than the distal cell, and the adaxial hairs with the distal cell shorter than the basal cell, resemble the microhairs of *P. malouinensis* of the *P. colorata* complex of Group 3 (Figure 48.3B, E). These microhairs differ considerably from the slender, elongated hairs with minute distal cells of Group 4.

The relationships of *P. capensis*, therefore, remain obscure and further studies of the other taxa of this Group 5 are needed before any deductions can be made. It is also probable that, even in the event of this material being available, little additional evidence will be forthcoming due to the very specialized habitat and resultant adaptations in the leaf anatomy which tend to mask the basic leaf architecture of *P. capensis*.

SPECIMENS EXAMINED

CAPE.—3318 (Cape Town): Table Mtn, Platteklip Gorge, (—CD), Ellis 5571, 5574. 3319 (Worcester): Waaihoek Peak, (—AD), Esterhuysen 2257; Franschhoek, Adolfskop, (—CC), Linder 4600. 3419 (Caledon): Vogelgat, (—AD), Schlechter 9520.

64 *P. andringitrensis* A. Camus p. 305 (Linder & Ellis 1990a: 104)

This distinctive species is very poorly known. It has only been recorded from Mt Andringitra in Madagascar and nothing is known of its ecology. No fixed leaf material was available for study and the preparations from reconstituted herbarium material were not very satisfactory. Leaf material in FAA would be extremely useful in gaining a better understanding of the anatomy of this species and of its relationships with the rest of the genus.

The anatomy of *P. andringitrensis* resembles that of *P. capensis* in several respects. The adaxial ribs are massive and flat-topped with deep, steep-sided furrows and the adaxial epidermal cells appear to be inflated (Figure 64.1A). However, these do not appear to represent globose papillae similar to those present on *P. capensis* (Figure 62.1). The leaf, although inrolled, is of the expanded type and the abaxial epidermal cells are noticeably larger than the adaxial cells. The abaxial epidermis has clear zonation, is without stomata, microhairs are common and the silica bodies are irregularly dumbbell-shaped (Figure 64.B). The abaxial microhairs have the two cells about equal in length.

Despite these similarities there are also anatomical differences between *P. andringitrensis* and *P. capensis*. Examples are the thick-walled sclerenchyma girders and the alternating large and smaller vascular bundles (Figure 64.1A). Of extreme significance appears to be the chlorenchyma tissue which, despite its very poor reconstitution, is apparently of the mesic type, suggesting that *P. andringitrensis* may actually belong to either of the glandular species groups 1 and 2. This can only be confirmed by examination of freshly fixed material.

The very inadequate anatomical evidence is, therefore, inconclusive and the relationships of this species remain obscure. Its tentative classification in this eglandular group seems to be the best course of action until additional information becomes available.

SPECIMENS EXAMINED

Locality unknown: Perrier 10832, Humbert 3919.

65 *P. humbertii* A. Camus p. 305 (Linder & Ellis 1990a: 105)

This is another very poorly studied species from Madagascar. Only the type specimen was available for anatomical study and only transverse sections were made. Rehydration, although poor, was adequate for anatomical interpretation.

The anatomy of *P. humbertii* compares very well with that of *P. andringitrensis* and these two species appear to be correctly placed together in the same species group. However, it is not possible to determine whether they belong to the glandular *Pentaschistis* groups (Groups 1 and 2) or not. Although no foliar glands were observed, the mesophyll appears to be of the mesic type despite the inadequate reconstitution of this tissue. This appears to indicate that the affinities of *P. humbertii* do lie with the glandular *Pentaschistis* species and not here in Group 5.

Anatomically *P. humbertii* is so similar to *P. andringitrensis* that the discussion and description of that species applies to this species as well. The only apparent difference between these two taxa is that the sclerenchyma girders are not as well developed in *P. humbertii*, an attribute which is very variable throughout the genus. An increased sample would undoubtedly reveal intermediate states of this character.

SPECIMEN EXAMINED

Locality unknown: Humbert 3310.

Group 6

All species of uncertain affinity are placed in this group. No morphological characters are diagnostic for these taxa and they all differ considerably in their morphology. A similar situation is reflected in the leaf anatomy and no unifying features characterize this group.

However, in contrast to the morphology, the leaf anatomy of two of these three unusual species does resemble that of other *Pentaschistis* taxa very closely, suggesting that they should be transferred from this group. Thus *P. heptamera* shows overall anatomical similarities with *P. pallida* form C and *P. papillosa*, both of Group 1. Indications are that these taxa belong together despite the absence of glands and the multiple-awned lemmas of *P. heptamera*.

Similarly, *P. eriostoma* seems to be related to *P. pyrophila* of Group 3, to *P. curvifolia* and the other taxa of

Group 4 as well as certain *Pentameris* species. This realignment would bring about uniformity in leaf anatomy amongst all these taxa but the morphological congruence would not be particularly close.

The affinities of *P. chrysurus* are not apparent from the small sample of poorly preserved material studied and the leaf anatomy does not suggest close relationships with any of the southern African species.

66 *P. chrysurus* (K. Schum.) Peter

p. 305 (Linder & Ellis 1990a: 105)

P. chrysurus is a montane species from the mountains in Tanzania in East Africa. It is a tall caespitose grass resembling the *Merxmuellera* species from the Drakensberg in growth form.

Little material was available for anatomical study and this material proved to be very brittle, making sectioning very difficult. However, from the sections obtained it was possible to determine that the leaf blade is of the expanded type, although subject to inrolling. The transverse sections resemble those of *Pentameris dregeana* rather closely (Ellis 1986a), particularly those specimens identified as *Pentastichis colorata* var. *polytricha* and illustrated in Ellis (1986a: figures 25 & 27). Reference to these illustrations will give a good indication of the transectional leaf blade structure of *P. chrysurus* but this similarity does not seem to imply taxonomic affinity.

Adaxial ribs and furrows are prominent, with the ribs associated with the first order bundles being slightly larger than the third order ribs. First and third order bundles alternate although a single second order bundle is present on either side of the median bundle which is indistinguishable structurally from the lateral first order bundles. There are seven first order bundles in the leaf transection. The bundles are associated with prominent adaxial and abaxial sclerenchyma girders, the fibres being lignified. The mesophyll tissue, although poorly reconstituted, appears to be of the sclerophyllous type, but this needs confirmation using freshly fixed collections.

The abaxial epidermis of *P. chrysurus* is illustrated in Figure 66.1. This shows clearly the absence of epidermal zonation, stomata, microhairs and other epidermal appendages. The long cells are relatively short and separated from adjoining cells by tall and narrow cork silica cell pairs. Sometimes these short cells may be in groups of four or five cells (Figure 66.1B) and then superficially resemble the translucent, short, sessile linear glands present in *P. velutina* (Figure 33.2). This possibility cannot be totally rejected but does appear unlikely. The abaxial epidermides of these two species, *P. chrysurus* and *P. velutina*, are very similar indeed (Figures 33.2; 66.1) but additional material of *P. chrysurus* is required before affinities between *P. chrysurus* and Group 2A can be considered. It is not possible to make meaningful deductions from inadequate samples as is the case with *P. chrysurus* and additional material is required to elucidate the relationships of this species. Until this happens it is advisable to leave this species in this group of species of uncertain affinity.

SPECIMEN EXAMINED

Locality unknown: *Volgens 1826a*.

67 *P. heptamera* (Nees) Stapf

pp. 306, 307 (Linder & Ellis 1990a: 106)

This species is restricted to maritime habitats, either in coastal sands or calcareous rocks, in the eastern Cape from Humansdorp to East London. It is found immediately above the high water mark where it is subject to salt spray.

Although *P. heptamera* is morphologically distinct on account of its multiple-awned lemmas, it is nevertheless sometimes confused with *P. pallida* form C which superficially resembles *P. heptamera* and shares similar habitats, extending eastwards as far as the Humansdorp District. The morphological resemblance between these two taxa is accorded no taxonomic significance and *P. heptamera* is included with the glandular species of uncertain affinity in Group 6, whereas *P. pallida* form C is placed in Group 1 with the glandular species, despite it being glandless.

The anatomy disagrees with this classification and supports a very close relationship between these two taxa. They share almost identical leaf anatomy and both are eglandular but have the same type of rather compact but nevertheless mesic chlorenchyma, indicating that their affinities probably lie with the glandular *Pentastichis* species of Group 1. This possibility is further supported by the anatomical resemblance of these two taxa to *P. papillosa*, a species which rarely has foliar glands and shares a similar habitat with *P. heptamera* and *P. pallida* form C. These three taxa, all from coastal habitats, are all anatomically very similar. The absence of glands in *P. heptamera*, and in *P. pallida* form C, seems to be a secondary reduction, considering the rare occurrence of glands in *P. papillosa*.

The fact that these three taxa all share a similar, and rather specialized maritime habitat, may have resulted in anatomical convergence in response to specific environmental factors operative in this habitat. Salt may be an example. If this is so, then the anatomical similarities between them may not be indicative of phylogenetic relationships. A complete synthesis of all characters is needed to resolve this possibility but, until such studies are undertaken, it seems reasonable to place *P. heptamera* together with *P. pallida* form C and *P. papillosa* in the same species group.

An unusual epidermal feature of *P. heptamera* and *P. pallida* form C is the occurrence of nuclei in virtually all epidermal cells (Figures 7c.2; 67.1E, F). Similar nucleate epidermal long cells also occur in both *P. ecklonii* and *P. reflexa* of Group 1E. Both these species are also without foliar glands and their leaf anatomy resembles that of *P. heptamera* in most respects. Differences are the abaxial stomata and microhairs, features which sometimes occur on *P. pallida* form C. It is possible that all these taxa should be united in a larger species group but the xerophytic anatomy of both *P. ecklonii* and *P. reflexa* seems to be a response to aridity, whereas similar anatomical adaptations in *P. heptamera* may be a response to salinity. This

type of anatomical convergence urges caution in placing too much emphasis on the anatomical evidence which may only reflect environmental influences and not phylogenetic lineages.

SPECIMENS EXAMINED

CAPE.—3326 (Grahamstown): Alexandria Dist., Kenton-on-Sea, (—DA), *Ellis* 6007. 3327 (Peddie): East London Dist., Christmas Rock, (—BA), *Ellis* 6008, *Acocks* 21839.

69 *P. eriostoma* (Nees) Stapf

pp. 308–312 (Linder & Ellis 1990a: 106)

P. eriostoma is unusual in the genus in being very widespread in the western and southern Cape Province, extending from the Kamiesberg in the west as far eastwards as Fort Beaufort in the eastern Cape. It inhabits a wide range of habitats throughout this distributional range and occurs from near sea level to alpine habitats as high as 1 800 m in various substrates such as shale, granite or sandstone derived soils. Generally *P. eriostoma* is found in dry situations, often on northern aspect slopes.

The leaf anatomy of *P. eriostoma* is typically xerophytic with the blade inrolled and often cylindrical (Figure 68.1A–F). The leaf margins are often asymmetrical and appear to act as a seal when inrolling occurs (Figure 68.1D, F). A well-developed abaxial hypodermal layer is often present (Figure 68.1E–H). No abaxial stomata are present (Figure 68.2) and the adaxial stomata are located on the bases and sides of the narrow furrows over which the prickles interlock (Figure 68.3B, E). All these features are often associated with xeric conditions and support the arid habitats favoured by this species. This anatomy is clearly illustrated in Robbertse (1959) under both *P. eriostoma* and *P. juncifolia*.

Of all the *Pentaschistis* species examined, *P. eriostoma* is most similar to *P. pyrophila* (Figures 44.1–44.3) of Group 3 in leaf blade anatomy. *P. pyrophila* differs from all the other taxa of Group 3A in a number of anatomical attributes, all of which it shares with *P. eriostoma* (Figure 68.1). These characters in combination serve to separate these two species from all other species groups in *Pentaschistis*. Examples are the alternating sequence of different orders of vascular bundle across the leaf width, the abaxial hypodermal layer and the characteristic elongated sclerenchyma girders. The abaxial epidermal cells are all uniform in size and are larger than the adaxial ones.

These two species also share numerous distinguishing epidermal features (Figures 68.2; 44.2): abaxial zonation is not evident, the cells are arranged in a brickwork pattern with the long cells alternating with cork-silica cell pairs, the silica bodies are rounded in shape and abaxial stomata, microhairs and other appendages are absent. The adaxial epidermis of these two species is also virtually identical

(Figures 68.3; 44.3) with very long and slender microhairs with minute distal cells and numerous prickly hairs.

The anatomy, therefore, strongly supports the grouping together of *P. eriostoma* and *P. pyrophila* in a separate species group. These two species share many features with *P. curvifolia* and its allies (Group 4) and the relationships of *P. eriostoma* appear to lie with this group of species. The only feature which *P. eriostoma* and *P. pyrophila* do not share with the *P. curvifolia* group of species is the thickened margins which are so characteristic of the *P. curvifolia* group. However, close examination of many of the sections of *P. eriostoma* does show that the lateral parts of the blade tend to be thicker than the median parts (Figure 68.1A, C, E) and a continuum therefore exists to the exaggerated condition present in *P. curvifolia*. This, together with all the other attributes shared between *P. eriostoma* and the *P. curvifolia* species group, supports close links between all these taxa.

The affinities of all these *Pentaschistis* taxa appear to be closer to several species of *Pentameris* than to any other group in *Pentaschistis*. The *P. eriostoma* type of anatomy, therefore, resembles that of *Pentameris longiglumis* (Ellis 1985b), *P. macrocalycina* and *P. obtusifolia* (Ellis 1985d) in many respects (the adaxial epidermal ultrastructure in particular) and all these taxa appear to constitute a homogeneous anatomical grouping. Further systematic studies are required to establish whether these anatomical indications are supported by other character distribution patterns.

The leaf anatomy of *P. eriostoma* is rather variable, which is consistent with such a widespread species occurring in so many different habitats. Several specimens consistently have abaxial macrohairs as illustrated in Figure 68.4. These specimens all come from silcrete substrates in the Bredasdorp District and may represent a distinct ecotype or taxon, possibly representing *P. juncifolia*. The illustrations of Robbertse (1959) of this taxon also have these superficial macrohairs. Further exploration is needed to determine the exact identity of these specimens with this slightly anomalous, but yet distinct, anatomy.

SPECIMENS EXAMINED

CAPE.—3018 (Kamiesberg): Kamiesberg, Rooiberg Peak S of Leliefontein, (—AC), *Ellis* 5402. 3119 (Calvinia): Koba Mts, Bokkeveld range, (—CA), *Ellis* 2444, 2446. 3218 (Clanwilliam): Piketberg, summit of Versfeld's Pass, (—DC), *Ellis* 1177; Piketberg Dist., Versfeld's Pass, lower slopes, (—DD), *Ellis* 5128. 3219 (Wuppertal): Cederberg, Sneeuksop Peak, (—AC), *Ellis* 5513; Koue Bokkeveld Mts, 16 km from Citrusdal, (—CA), *Ellis* 2491; Skurweberge, Blinkberg Pass, (—CD), *Ellis* 2502. 3319 (Worcester): Schurftberge, Gydo Pass, (—AB), *Ellis* 2486; Swartrugensberge, (—BA), *Ellis* 2473; Rawsonville, (—CB), *Ellis* 1251. 3321 (Ladismith): Swartberg, W of Waboomsberg, (—BD), *Ellis* 5627. 3322 (Oudtshoorn): Swartberg, Swartberg Pass, (—AC), *Ellis* 2581; Robinson Pass, (—CC), *Ellis* 2584. 3325 (Port Elizabeth): Uitenhage, (—CB), *Davidse* 33577. 3420 (Bredasdorp): 4 km from Bredasdorp turnoff on Swellendam-Riviersonderend road, (—AA), *Ellis* 1264; 5 km from Wydelegen on road to Malgas, (—AD), *Ellis* 1297, 5152, 5455; Malgas, (—BD), *Ellis* 667, Breede River mouth, *Ellis* 1672.

Anatomical species groups

The detailed leaf anatomy presented here was extensively used in the circumscription of species in a recent revision of the genus *Pentaschistis* (Linder & Ellis 1990a). This anatomical information proved invaluable in defining specific taxon limits and, consequently, there is generally close congruence between leaf anatomy and morphology at the species level in the genus. This is evident from the preceding anatomical discussion of the species.

In the taxonomic revision (Linder & Ellis 1990a) the species are grouped into reasonably uniform morphological groups which were established merely to facilitate identification of the species, and do not have phylogenetic, or any other, significance. However, these morphological groups often include species with differing anatomical features. Species groups based on uniform shared anatomical features would differ considerably in composition from the morphologically based groups. In the preceding anatomical treatment, which follows the sequence of taxa (and species groups) used in the revision, species with similar anatomy are therefore not necessarily grouped together. It follows that anatomical and morphological groups do not coincide as closely as the species circumscriptions do. Instead, species with similar anatomy are often grouped far apart, even in different species groups.

In this discussion all the species studied in sufficient detail are grouped into anatomical groups (Groups A–G) based on shared anatomical features, and their composition is compared with the species groups based on overall morphology (Groups 1–6). A summary of these species groups, together with the most important anatomical distinguishing features of each of the groups recognised, is given in Table 3 (p. 74).

Group A

Anatomical characteristics

Anatomical type: **typical mesic type**; expanded leaf blades; **margins abrupt**, not tapering; more rigid leaf blades with thick cuticles in subgroup Ae.

Glands: **stalked clavate multicellular glands** with elongated subglandular stalk cells common on leaf margins; domed adaxial glands may be present (subgroup Ad); foliar glands may be absent (subgroups Aa and Ae).

Mesophyll: **diffuse chlorenchyma**; cells loosely arranged, irregular in size and shape and with intercellular air spaces; **outer bundle sheath cells inconspicuous**, often containing unspecialized chloroplasts.

Vascular bundle arrangement: **alternating first and third order vascular bundles**; two smaller bundles may be present between the median bundle and the first lateral first order bundle.

Sclerenchyma: abaxial and adaxial strands or girders associated with all vascular bundles or only with the larger bundles; may be laterally expanded to trapezoidal but not fused laterally to form a hypodermal layer (except very rarely in subgroup Ae).

Abaxial epidermal cells: **similar in size and shape to adaxial cells**; usually rectangular in shape with sinuous walls but may be hexagonal in some specimens of both *P. densifolia* and *P. pallida* form F.

Adaxial epidermal cells: with inflated periclinal walls but not papillate.

Abaxial zonation: **always developed**; costal zones usually much narrower than intercostal zones, being only 1–3 files wide; costal zones wider in more xeric specimens of Group Ae.

Silica bodies: **dumbbell-shaped**, often very variable and tending to nodular type.

Microhairs: **small** (less than 2× the length of the stomatal complexes); somewhat longer in *P. capillaris*; finger-like with **distal cell equal in length to basal cell** or only slightly shorter.

Macrohairs: present or absent (subgroups Ab and Ac); two distinct types distinguishable:

- i) stiff hairs with constricted bases embedded in a raised cushion of modified epidermal cells (subgroup Ab);
- ii) flexible hairs with slightly swollen bases superficially associated with 1–4 inflated epidermal cells (subgroup Ac).

Prickles: very small adaxial hooks rare; well-developed adaxial prickles only on *P. barbata* subsp. *barbata* of Group Ae.

Abaxial stomata: **always present** except very rarely in the sandveld and strandveld forms of *P. barbata* subsp. *barbata* of Group Ae.

Group A contains only taxa from morphological Group 1, namely all those taxa with stalked glands. This gland type is closely correlated with the mesic type of anatomy

TABLE 3.—The most important distinguishing features of the leaf anatomy of the species groups of *Pentstemon*

Anatomical species groups														
Aa	Ab	Ac	Ad	Ae	Ba	Bb	Bc	Bd	Be	Ca	Cb	D	E	F
Mesic anatomy														
Tending to intermediate type with more compact mesophyll of uniform, angular cells with small air spaces														
Intermediate anatomy Sclerophyllous outline with diffuse chlorenchyma														
Sclerophyllous anatomy Compact chlorenchyma														
Eglandular														
Glandular														
Not stalked; lacking subglandular and collar cells														
Inflorescence glands only														
Rare or absent														
Sessile or elliptical														
Saddle														
Sunken														
Rare or absent														
Broad and short; distal cell longer than basal cell														
Short; distal and basal cell equal														
Short; broad; distal cell relatively large														
Elongate; slender; distal cell minute														
Zonation rarely developed														
Zonation developed														
Zones not differentiated														
Elliptical to tall and narrow cork-silica cell pairs														
Elliptical to irregularly dumbbell-shaped														
Typical dumbbell-shaped														
Always present														
Usually absent														
Always absent														
Few—many short prickles														
Absent														
Common; typical prickles or macrohair-like														
Sclerenchyma associated with larger bundles only; hypodermis often developed														
Large girders; not lignified														
Large girders; lignified														
Fused girders; thickened margin														
Strands or girders (rarely fused to form hypodermis); lignified or of cellulose; margin tapering or a narrow projection														
Hypodermal layer sometimes present														
Strands or girders; lignified or of cellulose; abrupt margin														
Common, well developed														
Sometimes absent														
Always present														
Absent, or few hook-like														
Common, well developed														
Hypodermal layer sometimes present														
Strands or girders; lignified or of cellulose; abrupt margin														
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with the chlorenchyma cells diffusely arranged. The individual chlorenchyma cells also differ considerably in size and shape. The outer bundle sheath cells of this group contain unspecialized chloroplasts. Other diagnostic features of this group are the abrupt, untapering leaf margins and the small size of the microhairs.

Some Group 1 taxa, however, are not placed in Group A. These are mostly taxa in which the glands are raised but do not have collar cells and subglandular tissue, that is, they are of the sessile elongated type. Without anatomical evidence it is often not possible to separate this gland type from the stalked gland type and this is a reason for the lack of congruence between the morphological and anatomical species groupings. Anatomically the taxa with sessile elongated glands have been assigned to Group Bb, Bc and Bd (Table 3). The Group 1 taxa with sunken, crateriform glands have also been removed from this group and placed in Group Bd.

A few anomalous Group 1 taxa, such as the high altitude form of *P. pallida* form B, *P. lima* and *P. cirrhulosa*, have even been transferred to Group C. These taxa invariably lack foliar glands, and therefore do not fit into Group A.

Species delimitations and specific limits in Group 1 proved very difficult to define unambiguously (Linder & Ellis 1990a) and an identical situation was revealed by the leaf anatomy. Thus different specimens of many taxa are accommodated in different anatomical subgroups of Group A. *P. pallida* form F 'pillansii', for example, has specimens assigned to Groups Aa, Ab, Ac, Ad and Ae. It is not surprising that the congruence between leaf anatomy and morphology at the species level breaks down more often in this group than in any other group. Assignment of the Group A specimens to taxa, based on anatomical circumscription of these taxa, would result in different delineation of these Group A taxa because the anatomical and morphological character sets do not coincide very closely.

In addition, the seven morphological subgroups of Group 1 are also not strongly supported by the anatomical evidence. This is mainly because habit, whether the plants are annual or perennial, does not appear to be strongly correlated with anatomical character distributions. Thus Groups 1A, 1B and 1C are separated by being strongly perennial, weakly perennial and annual. However, anatomical character distribution patterns are not correlated with habit and Groups Aa, Ab and Ac all contain both annual and perennial representatives.

This group is virtually restricted to the winter rainfall region of the Cape province, and concentrated in the fynbos biome. Several taxa extend as far as the arid fynbos bordering the karoo and there is a strong representation of Group A taxa in the Succulent Karoo in Namaqualand, with low precipitation occurring mainly in winter. This group is very poorly represented in the uniform rainfall areas to the east of the winter rainfall area, where Group B taxa are much more abundant.

Taxonomically this is the most difficult group in *Pentaschistis* and it will require more detailed work to resolve specific boundaries more satisfactorily. The ana-

tomical and morphological evidence is more conflicting than in any other group, reflecting this underlying taxonomic difficulty. Consequently the circumscription of the subgroups is less definite than in the other anatomical species groups, and their separation often depends on characters which may be variable.

Subgroups and included taxa

Group Aa

Few or no foliar glands; macrohairs very rare; xeric anatomical adaptations with well-developed girders, prominent adaxial ribs and furrows and relatively short intercostal long cells with thickened walls (cf. Group Ab).

This group includes plants from both Groups 1B and 1C, namely both annuals and perennials. All these plants are from drier areas with relatively fertile soils in the renosterveld and arid fynbos. The xeric anatomy of this group may also sometimes be a response to grazing. Correlated with the xeric anatomical adaptations is a reduction in the size and number of glands and macrohairs. Specimens placed in this subgroup may, therefore, only be ecotypes of Groups Ab and Ac which have lost the diagnostic macrohairs separating these latter two subgroups. However, the annual species, *P. patula* form A and *P. aristifolia*, are both consistently eglandular and without macrohairs, suggesting that the separation of this group is indeed justified.

Included taxa:

7 <i>P. pallida</i> form A 'brevifolia'	Group 1B
7 <i>P. pallida</i> form B 'pallida', xeric specimens	Group 1B
7 <i>P. pallida</i> form F 'pillansii', few specimens	Group 1B
12 <i>P. patula</i> form A 'patula'	Group 1C
13 <i>P. aristifolia</i>	Group 1C

Group Ab

Stalked foliar glands common; macrohairs stiff with constricted bases inserted into raised cushion bases composed of numerous modified epidermal cells; mesic anatomy with small sclerenchyma girders, wider adaxial furrows and longer intercostal long cells (cf. Group Aa).

This group forms the core of Group A and is very common in the heartland of the fynbos biome, viz. the area south of Porterville extending as far eastward as Caledon. Both perennial and annual species are included and thus taxa from Groups 1A, 1B and 1C are placed in this subgroup. The very variable but common specimens assigned to the mesic type of *P. pallida* form B, which is the commonest taxon in *Pentaschistis* in the south-western Cape, form the bulk of the material assigned to this group.

The macrohairs with their raised, cushion bases are diagnostic for this subgroup. However, this hair type does occur in other species groups such as Group B and rarely in Group E where the gland type differs or where glands are absent.

Included taxa:

- 1 *P. veneta*
- 2a *P. barbata* subsp. *barbata*, montane form
- 7 *P. pallida* form B 'pallida', mesic specimens
- 7 *P. pallida* form F 'pillansii', few specimens
- 8 *P. densifolia*
- 12 *P. patula* form C 'heteroplo'

- Group 1A
- Group 1A
- Group 1B
- Group 1B
- Group 1B
- Group 1C

Group Ac

Stalked foliar glands common; flexible macrohairs superficially inserted into a base of 1–4 inflated epidermal cells.

This subgroup also includes both annual and perennial taxa from Groups 1B and 1C. It dominates in the western and northern regions of the winter rainfall region, particularly the strandveld and Namaqualand.

The macrohairs of this subgroup differ substantially from those of subgroup Ab and consistently separate these two subgroups. However, these hairs are structurally very similar to those of some Group B taxa. In Group Bd, where the glands are sunken and crateriform, the hairs are stiffer than those of Group Ac but the macrohairs of *P. trisetata* and *Prionanthium* of Group Ba are identical to the hairs of this group. However, Group Ba has linear, sessile glands. This macrohair type is therefore not correlated with a particular gland type.

Included taxa:

- 7 *P. pallida* form F 'pillansii'
- 10 *P. tomentella*
- 13a *P. airoides* subsp. *airoides*
- 14 *P. capillaris*

- Group 1B
- Group 1B
- Group 1C
- Group 1C

Group Ad

Shared possession of the domed adaxially located type of gland with no surface detail.

All plants are from Namaqualand or the northern Cederberg (Olifants River Mountains) on granitic or humic black soils. This group does not correspond with any morphological taxon and includes a few specimens from four different taxa all from the same general geographical area and may merely represent an edaphic group with all specimens sharing this unique gland type. Its recognition as a separate subgroup of Group A is somewhat tentative but draws attention to these specimens sharing these unusual adaxially located glands.

Included taxa:

- 1 *P. veneta*, single northern specimen
- 2a *P. barbata* subsp. *barbata*, northern strandveld form
- 7 *P. pallida* form F 'pillansii', specimens from Olifants River area
- 10 *P. tomentella*, specimens from southern Namaqualand

- Group 1A
- Group 1A
- Group 1B
- Group 1B

Group Ae

Rigid leaves with thick abaxial cuticle; gland presence variable and foliar glands often rare or absent; no abaxial macrohairs; hypodermal sclerenchyma may be

developed and abaxial stomata often absent; thickened, sinuous anticlinal long cell walls; adaxial prickles common.

All specimens included in this group appear to have xerophytic, and even halophytic, adaptations. Collections from the West Coast lowlands and from the Cederberg are included. Anatomically this forms a rather uniform group but this is not reflected in the morphologically based classification. All plants are perennial and most are included in Group 1A.

The anatomy indicates that this is indeed a distinct and separate group distinguished mainly by xerophytic anatomical features. Thus the leaves are rigid with thick abaxial cuticles, with well-developed abaxial sclerenchyma girders often fused to form a continuous hypodermal layer. This results in the abaxial zonation being indistinct and stomata may be absent on this surface. The abaxial long cells are also thick-walled, with very sinuous anticlinal walls.

Correlated with this xeric type of anatomy is a definite reduction in gland presence (foliar glands are often totally absent) and macrohairs are also absent. A distinguishing feature of most specimens assigned to this subgroup are the well-developed adaxial prickles which may even interlock over the adaxial furrows. These prickles are not so well developed in the Cederberg specimens (*P. rupestris* and *P. pallida* form F). No other Group A taxa have this type of adaxial epidermis except for the Group Ad specimens. Subgroups Ad and Ae are undoubtedly very closely related and their unification may be justified.

Included taxa:

- 2a *P. barbata* subsp. *barbata*, sandveld form
- 2a *P. barbata* subsp. *barbata*, strandveld form
- 5 *P. rupestris*
- 7 *P. pallida* form F 'pillansii', some Cederberg specimens

- Group 1A
- Group 1A
- Group 1A
- Group 1B

Group B

Anatomical characteristics

Anatomical type: mesic but tending to intermediate type; expanded blade (except in *P. rosea* subsp. *rosea*) with **margin a narrow tapering projection** in Group Ba (except in *P. rosea* subsp. *rosea*) or **tapering** in Group Bb and Be but may be abrupt in Groups Bc and Bd.

Glands: linear (Group Ba), **sessile elongated** (Group Bb and Bc), **sunken crateriform** (Group Bd) or **raised but with subglandular tissue sunken in crypt** (Groups Bc, Bd, Be); **glands lack collar cells and subglandular (stalk) cells;** linear and crateriform glands abaxial or located along the margin; sessile glands abaxial or rarely adaxial (in *P. aurea* subsp. *pilosogluma*, *P. borussica* and *P. setifolia*) or along the margin where they may be slightly raised; saddle glands only in Group Bc.

Mesophyll: rather compact, of uniform, angular cells with reduced air space system to typical mesic type; **outer bundle sheath cells conspicuous and translucent** without chloroplasts; this character grades from Group Ba to Be where chloroplasts may be present in the outer bundle sheath cells.

Vascular bundle arrangement: alternating first and third order vascular bundles except on either side of the median bundle where 2 or 3 third order bundles occur.

Sclerenchyma: strands or girders associated with all bundles; not fused to form hypodermis except sometimes in Group Bd and Be.

Abaxial epidermal cells: similar in size to adaxial cells; larger in *P. pallescens* and *P. aurea*.

Adaxial epidermal cells: inflated outer walls but not papillate.

Abaxial zonation: clearly developed except in *P. pallescens* and species with hypodermal sclerenchyma.

Silica bodies: irregularly dumbbell-shaped to round or elliptical (Group Ba and *P. aurea* subsp. *pilosogluma*); nodular to dumbbell-shaped in Group Bb.

Microhairs: relatively large, from 2–4 times the length of the stomatal complexes; abaxial and adaxial; variable ratio of cell lengths with the distal cell longer than the basal cell, or the two cells of equal length, to distal cell slightly shorter than basal cell to very small distal cell and elongate basal cell; distal cell tapering.

Macrohairs: absent or long, flexible with slightly swollen base inserted between two epidermal cells, one of which is inflated (*P. trisetia* and *Prionanthium* and Group Bd only); thicker, stiffer hairs with small raised cushion bases in *P. pseudopallescens*, *P. pallescens*, *P. pallida* form G, *P. natalensis*, *P. papillosa* and *P. aspera*.

Prickles: small adaxial hooks in all groups; small abaxial costal prickles in Group Bd.

Abaxial stomata: irregular in occurrence, sometimes absent; dome-shaped; often deformed in Group Bb.

This species group differs substantially in composition from morphological Group 2. This results from a realignment of the glandular species of *Pentaschistis* as only species with stalked, clavate glands are retained in Group A, and all other gland types are accommodated in Group B. In the morphological classification only species with linear sessile glands were placed in Group 2; all other gland types were grouped in Group 1.

Group B does not include any taxa from morphological groups 3–6. However, all the Group 2a taxa are removed from Group B and placed in Groups C and D.

Many Group 1 taxa are placed in Group 2 on the basis of their gland structure: namely those taxa with elongated sessile glands grouped in Group Bb, the saddle glands of Group Bc and the crateriform glands of Group Bd. All these gland types were previously grouped together with the stalked, clavate gland type of Group 1 but here this latter gland type alone is restricted to Group A.

All gland types which consistently lack collar cells and subglandular tissue are grouped together here, in addition to the linear gland type which characterized morphological Group 2. This arrangement brings together all those *Pentaschistis* species with mesic anatomy but with tapering margins, colourless outer bundle sheath cells and with longer microhairs than those present in Group A. Although

the correlation is not perfect, this arrangement seems to reflect a more natural grouping than is the case when all species with raised glands are grouped together—irrespective of whether collar cells are present or not.

The grouping together of all gland types without collar and elongated subglandular cells appears at first glance to incorporate an excessive degree of variation. However, a distinct structural continuum exists from the linear sessile type through the elliptical sessile gland, raised elliptical glands with the subglandular tissue sunken in crypts and the sunken crateriform gland type. Taxa with any of these seemingly diverse gland types share a suite of other anatomical features (tapering margins, colourless parenchyma sheath cells and long microhairs) which are not present in Group A—which exclusively has the stalked, clavate gland type which in turn is correlated with abrupt margins, chloroplasts in the outer sheath cells and very tiny microhairs.

Group B also has a much more eastern distribution than does Group A and is concentrated in the uniform rainfall area around Knysna with a strong component extending up the eastern mountain ranges into the summer rainfall areas as far northward as Central Africa. Group A, by way of contrast, is concentrated in the heartland of the winter rainfall area, extending northwards into Namaqualand. Group Ba is an exception, being a genuine fynbos, winter rainfall group. Other coastal Group B taxa extend further westwards along the coast west of the Knysna area.

The species placed in Group B are generally much easier to define and circumscribe than is the case with Group A. Boundaries between the species are usually clear-cut and intermediates are few or absent. This applies to both morphological and anatomical criteria and, consequently, these two lines of evidence coincide very closely in this species group. The only exception is the distinction between *P. oreodoxa* and *P. setifolia*—two variable species which approach one another in both leaf anatomy and morphology and do not seem to be biologically separated (Linder & Ellis 1990a).

Subgroups and included taxa

Group Ba

Mesic anatomy with rather compact mesophyll of uniformly sized cells; sessile linear glands; margin a narrow, tapering projection; silica bodies very irregularly dumbbell-shaped to elliptical; abaxial stomata dome-shaped and subsidiary cells normal.

This group corresponds very closely to morphological Group 2B. Only *P. aurea* is excluded as the rare foliar glands of this species, although not raised, are of the sessile elliptical type and not linear, a gland type restricted to this subgroup.

Prionanthium has also been included in this group on the basis of the sessile linear glands on its leaves (Ellis 1989b). However, raised glands occur on the glumes of all three species of the genus (Davidse 1988). Although

raised, these glands appear to belong to the elongated gland type, as a clear transition is evident from slightly raised, elliptical glume glands on *P. pholiuroides* to stalked, oval glands on *P. dentatum* and *P. ecklonii* (Davidse 1988). The latter resemble the stalked, clavate gland type of Group A but anatomical studies are required to determine whether these glands are homologous and whether collar and stalk cells are present or not.

The close congruence between Groups Ba and 2B is not unexpected as both are based on the possession of linear glands. In Group 2A the linear glands are on the pedicels and not the leaf blades, and here the leaf anatomy and morphology are not in close agreement with the Group 2A species being placed in anatomical Groups Ca and even Da. Further anatomical studies on these glands is required before these taxa can be assigned to anatomical groups with reasonable certainty.

It is possible that Group Ba deserves the status of a species group on its own but the linear sessile gland appears to intergrade into the elongated sessile gland and further into raised gland types. *Prionanthium* clearly shows all types (Davidse 1988) and, consequently, all glands without collar cells are grouped together in Group B and this group is considered as a subgroup of Group B.

Included taxa:

36 <i>Pentastichis trisetia</i>	Group 2B
37a <i>P. rosea</i> subsp. <i>rosea</i>	Group 2B
37b <i>P. rosea</i> subsp. <i>purpurascens</i>	Group 2B
38 <i>P. pseudopallescens</i>	Group 2B
39 <i>P. pallescens</i>	Group 2B
<i>Prionanthium dentatum</i>	Ellis (1989)
<i>Prionanthium ecklonii</i>	Ellis (1989)
<i>Prionanthium pholiuroides</i>	Davidse (1988)

Group Bb

Mesic anatomy; elongated sessile glands but slightly raised in *P. pallida* form G and *P. barbata* subsp. *orientalis* absent; in *P. pallida* form D; margin tapering but not narrow projection (except *P. borussica*); silica bodies nodular to dumbbell-shaped; microhairs elongate, finger-like with short distal cell; macrohairs, when present, cushion-based; abaxial stomata often absent, when present dome-shaped but subsidiary cells often deformed.

This assemblage brings together taxa from several Group 1 subgroups as well as *P. aurea* from Group 2B. All these taxa proved difficult to place on morphology and the anatomical grouping brings together species from the summer rainfall region from tropical Africa as far southward and westward as the transitional area of the Knysna forests. However, specimens of these taxa from further west in the winter rainfall area do not agree with the definition of this Group. The western specimens of *P. ampla* and *P. aurea* subsp. *aurea* are good examples. These two species need further critical evaluation. It is possible that all the tropical African taxa from Group 1G also belong to this group but insufficient anatomical evidence is available at this stage.

Included taxa:

2b <i>P. barbata</i> subsp. <i>orientalis</i>	Group 1A
7 <i>P. pallida</i> form D 'australis'	Group 1B
7 <i>P. pallida</i> form G 'silvatica'	Group 1B
21 <i>P. borussica</i>	Group 1F
22 <i>P. natalensis</i>	Group 1F
25 <i>P. ampla</i> (particularly eastern specimens)	Group 1F
40a <i>P. aurea</i> subsp. <i>aurea</i> (eastern specimens)	Group 2B
40b <i>P. aurea</i> subsp. <i>pilosogluma</i>	Group 2B

Group Bc

Mesic anatomy with open, expanded blades; adaxial ribs well developed but furrows not cleft-like; raised, but not stalked, abaxial glands with saddle glands on the blade margin; margins rather abrupt; no hypodermal sclerenchyma; very large microhairs with distal and basal cells of equal length or distal cell longer than basal cell; abaxial stomata present.

This group contains two species, of which the affinities are unclear. They are tentatively placed together in this subgroup on the basis of their glands which, although raised, do not have the subglandular tissue elongated to form a stalk. They also have large microhairs.

The morphological similarity between *P. aspera* and *P. papillosa* is not supported by the leaf anatomy. *P. papillosa* shares more anatomical features with the Group Be taxa than it does with *P. aspera*.

Included taxa:

3 <i>P. aspera</i>	Group 1A
6 <i>P. longipes</i>	Group 1A

Group Bd

Mesic anatomy; crateriform glands with subglandular tissue sunken in crypts (apparently absent in *P. oreodoxa* and *P. pallida* form E); may be slightly raised in *P. oreodoxa*, *P. setifolia* and *P. pallida* form E; *P. galpinii* and *P. airoides* subsp. *jugorum* possess raised glands with subglandular tissue but this is sunken in a crypt; margins usually not tapering but narrow margins present in *P. pallida* form E and some specimens of *P. oreodoxa*; hypodermal sclerenchyma may be developed; microhairs elongate with short distal cell; macrohairs short, stiff and inserted into a superficial base of one or two inflated epidermal cells; abaxial costal prickles present; abaxial stomata absent except in *P. galpinii*, *P. microphylla* and *P. airoides* subsp. *jugorum*.

This subgroup contains mainly Group 1F taxa except for *P. pallida* form E. It appears to be a homogeneous grouping correlating very closely with the group based on morphological criteria after the removal of *P. borussica*, *P. natalensis* and *P. ampla* to Group Bb.

The inclusion of *P. galpinii*, *P. microphylla* and *P. airoides* subsp. *jugorum* in this group is tentative as they differ from the remainder in having raised glands and abaxial stomata, although not exclusively so. These three taxa form a close ecological grouping but cannot be satisfactorily separated from the rest of these Group Bd taxa

on the basis of anatomical character distributions. They may possibly be better placed in a separate subgroup together with *P. ecklonii* and *P. reflexa*—two taxa which also do not fit comfortably into Group Be.

The macrohairs of this subgroup resemble those of Group Ac very closely. In both groups these superficial hairs are inserted between a few distinctly inflated epidermal cells. These very distinctive hairs only occur in these two subgroups in the genus and are also uncommon elsewhere in the Poaceae. Despite the unusual nature of these hairs they are not correlated with other anatomical features and consequently are accorded very little taxonomic significance.

Included taxa:

23 <i>P. oreodoxa</i>	Group 1F
24 <i>P. setifolia</i>	Group 1F
26 <i>P. glandulosa</i>	Group 1F
7 <i>P. pallida</i> form E 'angustifolia'	Group 1B
17 <i>P. galpinii</i>	Group 1D
18 <i>P. microphylla</i>	Group 1D
13 <i>P. airoides</i> subsp. <i>jugorum</i>	Group 1C

Group Be

Mesic to somewhat intermediate type anatomy; expanded but inrolled leaves with large, flat-topped ribs and cleft-like furrows; ribs not so pronounced on *P. ecklonii* and *P. reflexa*; foliar glands absent (except rarely on *P. papillosa* where they are slightly raised); gently tapering margins; hypodermal sclerenchyma may be developed; microhairs elongate with small distal cell or the two cells of equal length; abaxial stomata present or absent; epidermal cells nucleate.

The taxa comprising this Group usually occur on calcareous soils, often associated with coastal dunes. This may account for the anatomical similarities shared by them although the three taxa are not sympatric. *P. papillosa* is an exception, being restricted to sandstones. The group is, nevertheless, distinctive enough to be grouped separately sharing a very uniform leaf anatomy.

It is debatable whether *P. ecklonii* and *P. reflexa* are correctly placed in this grouping as they do not share the same ecology as the other three taxa. They may be better placed in a separate group together with *P. galpinii*, *P. microphylla* and *P. airoides* subsp. *jugorum*. The absence of glands on the leaves of *P. ecklonii* and *P. reflexa*, which they share with Group Be, is the determining factor in the retention of these two taxa in this group.

Included taxa:

4 <i>P. papillosa</i>	Group 1A
7 <i>P. pallida</i> form C 'albescens'	Group 1B
67 <i>P. heptamera</i>	Group 6
19 <i>P. ecklonii</i>	Group 1E
20 <i>P. reflexa</i>	Group 1E

Group C

Anatomical characteristics

Anatomical type: sclerophyllous but without compact chlorenchyma; mesophyll cells larger than usual for the

sclerophyllous anatomical type and tend to be diffusely arranged; intermediate type; leaf blades setaceous except in *P. aristidoides*.

Glands: glandular (Group Ca) or eglandular (Group Cb); gland type variable but not typically stalked, clavate type.

Mesophyll: larger mesophyll cells; central vacuoles not present; intercellular air spaces present; possibly a modification of the mesic type.

Vascular bundle arrangement: alternating first and third order bundles; rarely with successive lateral larger bundles in *P. rigidissima* only.

Sclerenchyma: girders only associated with first order vascular bundles except in *P. chippindalliae*, *P. aristidoides* and *P. velutina*; abaxial hypodermal layer often present (but this usually not connected to the third order bundles).

Abaxial epidermal cells: only slightly larger than adaxial cells; cell walls thickened; no size difference between costal and intercostal epidermal cells; no cuticular papillae.

Adaxial epidermal cells: slightly smaller than abaxial epidermal cells; no inflated papillae; elongated cuticular papillae may occur on some Group Cb taxa (this needs confirmation).

Abaxial zonation: very rarely developed; present only on some specimens of *P. aristidoides* and *P. rigidissima*.

Silica bodies: elliptical to tall and narrow; cork-silica cell pairs located between long cells throughout the abaxial epidermis; in specimens with epidermal zonation, dumbbell-shaped silica bodies are present.

Microhairs: not finger-like; broad and short with distal cell relatively large—equal to or longer than the basal cell; rare on abaxial surface; adaxial microhairs elongate with very small distal cell in *P. aristidoides* and minute distal cell in *P. velutina*.

Macrohairs: absent except in *P. chippindalliae* and sometimes *P. aristidoides*.

Prickles: few to many short adaxial prickles; *P. lima* with numerous abaxial hooks.

Abaxial stomata: absent except irregularly on *P. lima* and some specimens of *P. aristidoides*.

This anatomical species group is truly intermediate between the two primary morphological subdivisions, namely the glandular species (Groups 1 and 2) and the eglandular species (Groups 3–6). The leaf anatomy of this group is also not typical of either the mesic or the sclerophyllous types but includes features of both. It is only in this species group that the very strong correlation between the occurrence of glands and the mesic type appears to break down. In fact it is the possession of glands in the Group Ca taxa which demand a detailed definition of the mesophyll of the sclerophyllous type in order to enable the two anatomical types to be consistently separated.

Included in this anatomical species group are several atypical glandular species which proved difficult to classify satisfactorily on morphological evidence. They comprise Group Ca and all have inflorescence glands and are, there-

fore, included in morphological species Groups 1 and 2. This anatomical grouping appears to be polyphyletic but very little is known about the glands of all the included taxa except some high altitude specimens of *P. pallida* form B, which is the only taxon of Group Ca with foliar glands. Raised as well as linear glands seem to be included in this group but it is uncertain whether the raised glands are typical of the stalked clavate type of Group A or the Group Bb raised, elliptical gland type which is without collar cells and subglandular tissue. It appears likely that the inflorescence glands of Group C will closely resemble the variable glands included in Group B but until this is satisfactorily determined it appears reasonable to assign these taxa to this intermediate, rather heterogeneous group.

Group Cb, on the other hand, contains only eglandular taxa, all from morphological species Group 3. It appears to be a natural grouping, mainly of summer rainfall species and several tropical African species probably also belong to this assemblage. There are also close anatomical resemblances to *Merxmuellera disticha* and its allies which suggest relationships between these taxa.

The links between Groups Ca and Cb do not appear to be very close but they are grouped together in the same anatomical species group due to the unusual nature of the mesophyll tissue which they share. This tissue of larger, angular chlorenchyma cells without central vacuoles differs considerably from the typical sclerophyllous condition and may be a modification of the mesic anatomical type. The leaves, which are setaceous and permanently infolded, possess many other features which are usually associated with the sclerophyllous anatomical type. Examples are the well-developed sclerophyllous girders often fused to form a hypodermal layer and the absence of abaxial epidermal zonation. With the exception of the chlorenchyma structure all the other features of the Group C anatomy agree with the sclerophyllous anatomical type of Groups D–F. Group C, therefore, is anatomically intermediate between Groups A and B (the mesic type) and Groups D–F (the sclerophyllous type).

Some shared features suggest that Groups Ca and Cb should be grouped together in a single species group. Examples are the alternating arrangement of large and small vascular bundles, the absence of girders associated with the smaller bundles, the elliptical silica bodies closely associated with enfolding cork cells and the microhairs which are not finger-like. All these features in combination only occur in this species group, and together with the unusual chlorenchyma, suggest that Group C may indeed be a natural grouping.

Subgroups and included taxa

Group Ca

Inflorescence glands present (except in *P. montana*); raised leaf glands only present on certain high altitude *P. pallida* form B specimens; short linear leaf glands on *P. velutina*; adaxial papillae absent.

This is a heterogeneous grouping which is also probably polyphyletic. Although *P. montana* is eglandular, its

removal from Group 3 seems justified on the basis of several characteristic features of Group C which it possesses. This species appears to be particularly close to the high altitude form of *P. pallida* form B. The position of *P. cirrhulosa* is particularly uncertain and it has also been placed in Group Ec with *P. calcicola*. Additional studies of this species are required before a more definite decision can be taken.

P. aristidoides, *P. velutina* and the undescribed species under *P. viscidula* (Ellis 5499, 5589) form a small but coherent group. It may be advisable to recognise this as a separate subgroup. These three taxa definitely do not belong together with *P. argentea* and *P. viscidula* which have been transferred to Group D.

Included taxa:

46 <i>P. montana</i>	Group 3A
7 <i>P. pallida</i> form B 'pallida', only high altitude specimens	Group 1B
11 <i>P. lima</i>	Group 1B
9 <i>P. cirrhulosa</i> (?)	Group 1B
32 <i>P. aristidoides</i>	Group 2A
33 <i>P. velutina</i>	Group 2A
34 Ellis 5499 and 5589 (Sp. under <i>P. viscidula</i>)	Group 2A

Group Cb

Eglandular; alternating first and third order vascular bundles; abaxial epidermal cells not much larger than adaxial ones; adaxial papillae absent; silica bodies elliptical.

All taxa, except *P. rigidissima*, are summer rainfall species. Although *P. exserta* superficially resembles *P. tysonii*, the leaf anatomy shows significant differences, so much so that these two taxa have been placed in separate species groups—Group Cb and Group Eb.

Strong links for Group Cb with *Merxmuellera disticha* and its allies (*M. davyi* and *M. macowanii*, Ellis 1981b) are indicated by the leaf anatomy. *M. disticha* and the Group Cb (and Ca) taxa share a suite of anatomical characters which do not occur elsewhere in either *Pentastichis* or *Merxmuellera*. This character distribution pattern suggests that new generic alignments are required to accommodate these anatomical indications. It is of interest to note that all three of these *Merxmuellera* species may be 2-flowered—a distinguishing feature of the genus *Pentastichis* (Gibbs Russell *et al.* 1990).

Included taxa:

47 <i>P. rigidissima</i>	Group 3A
53 <i>P. chippindalliae</i>	Group 3B
54 <i>P. exserta</i>	Group 3B
55 <i>P. basutorum</i>	Group 3B
<i>Merxmuellera disticha</i> , typical form	Ellis (1980a)
<i>M. disticha</i> , Drakensberg form	Ellis (1980a)
<i>M. disticha</i> , alpine bog form	Ellis (1980a)
<i>M. davyi</i>	Ellis (1981b)
<i>M. macowanii</i>	Ellis (1981b)

Group D

Anatomical characteristics

Anatomical type: sclerophyllous, typical anatomy of this type except for the presence of abaxial stomata; the leaves are also not of the permanently, infolded setaceous type.

Glands: foliar glands absent but linear glands rarely present on pedicels in *P. viscidula* and *P. argentea*; do not appear to occur on the *Merxmuellera* species.

Mesophyll: compact, small isodiametric cells with central vacuole; very small intercellular air spaces.

Vascular bundle arrangement: alternating large and small bundles.

Sclerenchyma: abaxial and adaxial girders always present; not fused abaxially; fibres not lignified.

Abaxial epidermal cells: equal in size to adaxial cells; costal and intercostal cells similar in size.

Adaxial epidermal cells: similar size to abaxial cells; slightly inflated but not papillate.

Abaxial zonation: costal and intercostal zones developed; structurally distinct.

Silica bodies: costal silica bodies irregularly dumbbell-shaped to elliptical.

Microhairs: present on abaxial and adaxial surfaces; relatively short and broad with distal cell only slightly shorter than basal cell.

Macrohairs: absent (*P. argentea*) or abaxial, superficial, intercostal macrohairs present (*P. viscidula*).

Prickles: few small adaxial hooks present.

Abaxial stomata: common; low dome-shaped stomata throughout all intercostal zones.

This anatomical species group does not correspond closely to any of the morphological groupings but, as presently constituted, forms a distinct and homogeneous anatomical group. Group D combines some of the *Pentastichis* species from Group 2A, which have linear glands and swollen villous bases, with *Merxmuellera* species with similar bases—*M. lupulina*, *M. rufa* and *M. decora*. These *Merxmuellera* species appear to lack linear pedicel glands and they also show growth form similarities with the *Pentastichis* species of Group 2A (Linder & Ellis 1990a). It is of interest that *M. lupulina* also sometimes has 2-flowered spikelets (Gibbs Russell *et al.* 1990).

Although *P. aristoides* and *P. velutina* have swollen villous bases, they have been excluded from this group as they do not have typical sclerophyllous anatomy with mesophyll tissue of compact, small isodiametric chlorenchyma cells with central vacuoles. These two species have tentatively been placed in Group Ca as their leaf anatomy differs somewhat from that of the taxa presently comprising this distinct anatomical species group.

Included taxa

Typical sclerophyllous anatomy except that abaxial stomata are very numerous; foliar glands absent; compact mesophyll of small isodiametric cells with central vacuoles; alternating first and third order vascular bundles; sclerenchyma not lignified; abaxial zonation with intercostal stomata; microhairs short with distal cell not minute.

This small but distinct group combines two *Pentastichis* species with three anatomically similar *Merxmuellera*

species which form an obvious subgrouping within the latter genus. The combination of these taxa into a separate anatomical group is supported by certain morphological criteria (such as the geophytic growth form shared by all the taxa) but other characters (such as number of florets per spikelet and linear pedicel glands) are then not uniform throughout this Group D. However, *M. lupulina* sometimes has 2 florets per spikelet (Gibbs Russell *et al.* 1990), a typical *Pentastichis* feature. The taxonomic composition and position of this group needs further detailed investigation.

Included taxa:

34 <i>P. viscidula</i>	Group 2A
35 <i>P. argentea</i>	Group 2A
<i>Merxmuellera lupulina</i>	Ellis (1983)
<i>M. rufa</i>	Ellis (1983)
<i>M. decora</i>	Ellis (1983)

Group E

Anatomical characteristics

Anatomical type: sclerophyllous, conforms with definition in all respects except Group Ec where mesophyll more diffuse.

Glands: eglandular; *P. cirrhulosa* (with inflorescence glands) only exception.

Mesophyll: small, compact, isodiametric chlorenchyma cells with central vacuole; air spaces minute; mesophyll differs in Group E—tends to mesic type.

Vascular bundle arrangement: alternating first and third order vascular bundles (Groups Ea and Ec) or larger lateral bundles not interspaced with third order bundles (Group Eb).

Sclerenchyma: lignified adaxial and abaxial girders associated with all vascular bundles; fusion of abaxial girders sometimes in Group Eb.

Abaxial epidermal cells: considerably larger than adaxial cells; walls not thickened; intercostal cells larger than costal cells except sometimes in Group Eb in specimens with hypodermal sclerenchyma; unique cuticular papillae may sometimes occur in Group Ea.

Adaxial epidermal cells: smaller than abaxial cells; papillate with inflated papillae except in Group Ec where papillae less well developed.

Abaxial zonation: intercostal and costal zones clearly differentiated except in Group Eb specimens with fused abaxial girders where zonation is not distinguishable.

Silica bodies: typical dumbbell-shaped to very irregularly dumbbell-shaped or elliptical in Groups Eb and Ec; confined to costal zones.

Microhairs: broad with distal cell relatively large, equal to or longer than basal cell; both abaxial and adaxial; no abaxial microhairs in Group Ec and distal cell shorter in Group Eb.

Macrohairs: usually absent; cushion-based hairs rarely present in Group Ea (*P. alticola* and *P. elegans*).

Prickles: few, small adaxial prickles present.

Abaxial stomata: absent.

Only taxa from Group 3 are included in this anatomical species group, with the possible exception of *P. cirrhulosa* which is dubiously included in both this group as well as Group Ca. Several other Group 3 *Pentaschistis* species have been excluded from Group E and placed in Group Cb. This supports the contention of Linder & Ellis (1990a) that Group 3 is not a monophyletic assemblage. Nevertheless, the anatomical and morphological features are in close agreement in the eglandular *Pentaschistis* species—much more so than was the case with the glandular species groups.

In addition to the Group 3 *Pentaschistis* species, *M. stricta* and its allies are also included in this assemblage on the basis of shared overall anatomical attributes. The Drakensberg form of *M. stricta* and the Cathedral Peak form of *M. guillarmodiae* (Ellis 1980b) show the greatest resemblance to the *Pentaschistis* species of this group but other species, such as the typical form of *M. stricta*, the alpine bog form of *M. guillarmodiae*, *M. stereophylla* and *M. drakensbergensis* (Ellis 1981b), appear to belong with this group as well. All these species share the unique inflated adaxial papillae. They also possess a similar sequence of arrangement of the vascular bundles where the lateral first order bundles are not interspaced with small bundles, a feature diagnostic of anatomical subgroup Eb of *Pentaschistis*.

It is of interest to note that none of the *Merxmuellera* species included in Group E have less than four florets per spikelet. This contrasts with the situation present in the *Merxmuellera* species included in Group Cb, where *M. disticha*, *M. davyi* and *M. macowanii* generally have less than four florets per spikelet—often with only two (Gibbs Russell *et al.* 1990a). The transfer of these *Pentaschistis* species (*P. rigidissima*, *P. chippindalliae* and *P. basutorum*) from Group 3 is, therefore, supported by both morphology and leaf anatomy.

This species group, as here constituted, seems to be a more natural grouping than Group 3. Group Ea, the *P. colorata* group of species, is undoubtedly a monophyletic assemblage. Whether this group should be placed in the same species group as Group Eb is not clear but they do share several significant anatomical features. Group Eb is also a homogeneous anatomical grouping with *P. tysonii*, *P. holciformis* and *P. praecox* sharing virtually identical anatomy with *M. stricta* and its allies.

Subgroups and included taxa

Group Ea

Mesophyll very compact of small vacuolate cells; **alternating large and small vascular bundles**; **intercostal and costal abaxial epidermal cells differ in size**; **unique abaxial papillae may be present**; **adaxial epidermal cells with conspicuous inflated papillae**; **distinct abaxial epidermal zonation**; **silica bodies typical dumbbell-shaped**; **microhairs with distal cell equal to or even longer than basal cell**.

Anatomically this is a remarkably uniform group and undoubtedly includes closely related taxa, all of which

were also included in the same morphological group (Group 3a). The only exception may be *P. pusilla* from which specimens forming tangled mats and with soft expanded leaves have been excluded. These specimens have been left ungrouped as they do not conform closely to any other *Pentaschistis* species. Linder & Ellis (1990a) noted that two taxa may be included in *P. pusilla*, an observation which is supported by the anatomical evidence.

The size difference between the costal and intercostal abaxial epidermal cells is a conspicuous and distinguishing feature of this group. The dumbbell-shaped silica bodies, together with the sclerophyllous type of leaf anatomy, also serve to distinguish this group. The abaxial cuticular papillae are a unique feature of some taxa in Group Ea, being found on some specimens of *P. colorata* and *P. alticola*. Abaxial papillae do not occur on any other southern African member of the Arundinoideae and are very rare in this subfamily (Renvoize & Clayton 1986; Watson & Dallwitz 1988).

Included taxa:

41 <i>P. colorata</i>	Group 3A
42 <i>P. tortuosa</i>	Group 3A
43 <i>P. alticola</i>	Group 3A
48 <i>P. malouinensis</i>	Group 3A
49 <i>P. pusilla</i> , only form with rolled leaves	Group 3A
50 <i>P. elegans</i>	Group 3A

Group Eb

Mesophyll very compact of small vacuolate cells; **lateral first order bundles not interspaced with third order bundles**; **abaxial sclerenchyma girders may be fused**; **abaxial costal and intercostal epidermal cells not always differing in size (linked to possession of hypodermal sclerenchymatous layer)**; **abaxial cuticular papillae absent**; **conspicuous adaxial inflated papillae**; **abaxial zonation not always evident (linked to possession of hypodermal layer)**; **silica bodies very irregular dumbbell-shaped to elliptical**; **adaxial microhairs with short distal cell—hairs not slender, elongate**.

The three *Pentaschistis* species included in this grouping are indistinguishable in leaf anatomy from *Merxmuellera stricta* and its allies. This applies particularly to the Drakensberg form of *M. stricta* and the Cathedral Peak form of *M. guillarmodiae* (Ellis 1980b: figures 29–32). These illustrations, together with those presented in the anatomical treatment of the species in this paper, show unambiguously that *P. tysonii*, *P. holciformis* and *P. praecox* share very similar leaf anatomy with these *Merxmuellera* species and that similar leaf anatomy does not occur elsewhere in *Pentaschistis*. Their accommodation in the same species group results in homogeneous leaf anatomy. Linder & Ellis (1990a) note that these *Pentaschistis* species show affinities with some species of *Merxmuellera*, but, as they consistently have two florets per spikelet, they were retained in *Pentaschistis*.

The pattern of arrangement of the vascular bundles across the leaf blade serves to distinguish this group. Laterally the first order bundles are not separated by third order bundles, a feature unique to this grouping. The abaxial

costal and intercostal cells do not differ in size as seen in transverse section as in Group Ea. The adaxial epidermal cells with conspicuous, inflated papillae are very similar to those of Group Ea and this supports the retention of these two groups in a single species group.

Included taxa:

51 <i>P. tysonii</i>	Group 3B
52 <i>P. holciformis</i>	Group 3B
56 <i>P. praecox</i>	Group 3B
<i>Merxmüllera stricta</i> , Drakensberg form	Ellis (1980b)
<i>M. guillarmodiae</i> , Cathedral Peak form	Ellis (1980b)
<i>M. stricta</i> , typical form	Ellis (1981b)
<i>M. guillarmodiae</i> , alpine bog form	Ellis (1981b)
<i>M. stereophylla</i>	Ellis (1981b)
<i>M. drakensbergensis</i>	Ellis (1981b)

Group Ec

Sclerophyllous anatomy but mesophyll tissue of rather large cells without central vacuoles—possibly mesic type (*P. cirrhulosa*); inflorescence glands may occur (*P. cirrhulosa*); alternating vascular bundles; size of abaxial costal and intercostal epidermal cells differs very little; no abaxial cuticular papillae; adaxial epidermal inflated papillae not well developed or even absent; silica bodies irregular dumbbell-shaped and very variable in shape; no abaxial microhairs; adaxial microhairs with distal cell equal to basal cell.

This assemblage is not clearly defined and its constitution and composition is not convincing. *P. calcicola* may be better accommodated in Group Ca, another indistinct group exhibiting considerable character variation. This group (Ca) includes *P. montana*, another species without glands, which was also originally placed in Group 3a together with *P. calcicola* on morphological grounds. *P. cirrhulosa*, an atypical species from Group 1, has provisionally been placed in both groups Ca and Ec.

Both *P. calcicola* and *P. cirrhulosa* do not have typical sclerophyllous type mesophyll tissue, the chlorenchyma cells being larger than in the remaining taxa of Group E. Nevertheless these cells are uniform in size and compactly arranged, features which characterize the sclerophyllous anatomical type. This mesophyll may represent an extreme modification of the mesic type, and, if so, the included taxa should be transferred to Group Ca.

Included taxa:

45a <i>P. calcicola</i> var. <i>calcicola</i>	Group 3A
45b <i>P. calcicola</i> var. <i>hirsuta</i>	Group 3A
9 <i>P. cirrhulosa</i> (?)	Group 1B

Group F

Anatomical characteristics

Anatomical type: sclerophyllous, leaves not permanently inrolled or setaceous; margins of lamina thicker than midlamina region.

Glands: eglandular (except possible linear glands in *P. pungens*).

Mesophyll: small isodiametric chlorenchyma cells with central vacuoles; minute intercellular air spaces.

Vascular bundle arrangement: alternating first and third order vascular bundles (pattern sometimes disrupted in thickened lateral part of lamina).

Sclerenchyma: adaxial and abaxial girders associated with all vascular bundles; **abaxial lateral fusion in thickened margin;** adaxial ribs inversely anchor-shaped, located in flat-topped ribs.

Abaxial epidermal cells: uniform in size and shape across leaf width (although cells wider laterally where blade is thickest); no size variation between costal and intercostal zones; **noticeably larger than adaxial cells** except in *P. acinosa* where the abaxial and adaxial epidermal cells are similar in size.

Adaxial epidermal cells: smaller than abaxial cells; not papillate but may be somewhat inflated, particularly in *P. acinosa*.

Abaxial zonation: costal and intercostal zones **not differentiated;** *P. acinosa* is only exception.

Silica bodies: elliptical or tall and narrow, always enfolded by associated cork cell; alternate with long cells throughout epidermis.

Microhairs: absent abaxially (except in *P. caulescens* where the two cells are about equal in size); **adaxial microhairs slender, elongated, finger-like with minute distal cell.**

Macrohairs: absent although elongate prickles of Group Fb resemble macrohairs.

Prickles: adaxial prickles present; typical prickles (Group Fa) or elongate and macrohair-like (Group Fb); may be very common and interlock over the cleft-like furrows.

Abaxial stomata: absent.

Anatomically this constitutes a very distinct group, clearly separable from all the other species groups. Diagnostic anatomical features include the sclerophyllous anatomy in expanded leaves, the thickening of the leaf blade in the region of the margin (particularly evident in Group Fa), the absence of epidermal zonation, the elliptical or tall and narrow silica bodies, the very elongate and slender adaxial microhairs with minute distal cells and the conspicuous adaxial prickle hairs (which even resemble macrohairs in Group Fb).

Group Fa coincides perfectly with morphological Group 4—the only instance of complete congruence between the leaf anatomy and the morphology in all the species groups in the genus. *P. curvifolia* and its allies form a discrete, homogeneous group which probably reflects close evolutionary relationships. *P. acinosa* is somewhat peripheral to this group but none of its features diverge sufficiently to cause the group to lose cohesion. It only differs in having relatively large adaxial epidermal cells and abaxial zonation is evident. The possible presence of linear marginal glands in *P. pungens* may be highly significant in establishing polarity in gland occurrence and will effect concepts of phylogeny in the genus. This species deserves further study.

Group Fa intergrades into Group Fb where thickened margins are not so conspicuous and where the adaxial prickles are more elongate and numerous. These two groupings appear to constitute a homogeneous species group even though the representatives of Group Fb do not form a uniform morphological entity, having been placed in Groups 3a and 6. *P. pyrophila* and *P. eriostoma* share several distinct features, such as the adaxial prickles and elongate microhairs with minute distal cells, that support their placement together in this group. Also included in Group Fb on the basis of very similar anatomy are four species of *Pentameris*, indicating that this species group may actually constitute a new and separate genus, notwithstanding the fact that the species of *Pentastichis* and *Pentameris* differ in ovary and fruit structure (Gibbs Russell *et al.* 1990).

Subgroups and included taxa

Group Fa

Lateral blade and leaf margin thickened throughout with median part of blade thinner than lateral part; adaxial ribs flat-topped and furrows narrow, cleft-like; adaxial surface with typical prickles (not elongate, resembling macrohairs).

P. curvifolia and its allies form a very discrete anatomical and morphological group which undoubtedly reflects evolutionary relationships. Little anatomical resemblance is displayed with any of the other species groups in *Pentastichis* but this subgroup shows close similarities with the species of Group Fb which includes several species currently classified in *Pentameris*.

Included taxa:

57 <i>P. curvifolia</i>	Group 4
58 <i>P. pungens</i>	Group 4
59 <i>P. acinosa</i>	Group 4
60 <i>P. caulescens</i>	Group 4
61 <i>P. scandens</i>	Group 4

Group Fb

Margins not conspicuously thickened (although slight lateral thickening may be evident in all species); adaxial surface with numerous elongated prickles—these may be regarded as macrohairs.

The taxa of this group are excluded from Group Fa due to the absence of conspicuously thickened leaf margins, although these do occur in *Pentameris longiglumis* (Ellis 1985b). This group also differs from Group Fa in possessing numerous, elongate adaxial prickles. The inclusion of *P. dregeana* in this group is tentative as these prickles are not common in this species. However, it does share woolly sheath mouths with *Pentastichis eriostoma*. The affinities of *Pentameris dregeana* are difficult to ascertain with any degree of certainty and await the synthesis of additional character sets. The characters separating the two subgroups of species Group F therefore are not mutually exclusive.

Included taxa:

44 <i>Pentastichis pyrophila</i>	Group 3A
68 <i>P. eriostoma</i>	Group 6
<i>Pentameris longiglumis</i>	Ellis (1985b)
<i>Pentameris macrocalycina</i>	Ellis (1985d)
<i>Pentameris obtusifolia</i>	Ellis (1985d)
<i>Pentameris dregeana</i>	Ellis (1986a)

Group G

This group includes all those species of uncertain affinity which cannot be accommodated in any of the other species groups. No common anatomical features are shared by the taxa included in this assemblage. Most taxa are included here because they are insufficiently known and, when more material becomes available for anatomical study, they will undoubtedly be assigned to several of the existing species groups.

Ungrouped species:

49 <i>P. pusilla</i> , specimens with expanded leaves	Group 3A
62 <i>P. capensis</i>	Group 5

Insufficient material/information:

16 <i>P. trisetoides</i>	Group 1C
27 <i>P. minor</i>	Group 1G
28 <i>P. mannii</i>	Group 1G
29 <i>P. imatongensis</i>	Group 1G
30 <i>P. pictigluma</i>	Group 1G
31 <i>P. gracilis</i>	Group 1G
63 <i>P. insularis</i>	Group 5
64 <i>P. andringitrensis</i>	Group 5
65 <i>P. humbertii</i>	Group 5
66 <i>P. chrysurus</i>	Group 6

Conclusions

This anatomical study of *Pentaschistis* clearly illustrates the exceptionally high degree of anatomical variation currently accommodated in the genus. The amount of anatomical variability is greater than in any other southern African arundinoid genus (and possibly any other grass genus apart from *Panicum*), suggesting that the genus is artificial as presently constituted.

If this anatomical study is compared to similar studies of other South African arundinoid taxa (Ellis references) it is immediately evident that several of the *Pentaschistis* anatomical types described here closely resemble the anatomy of other arundinoid taxa from different genera. These resemblances are often striking, the anatomy of *Pentaschistis* species being almost identical to certain other arundinoid taxa—some *Merxmuellera* and *Pentameris* species in particular, as well as *Prionanthium*. In these instances the *Pentaschistis* taxon resembles these neighbouring genera much more closely in leaf anatomy than it does any other *Pentaschistis* taxon, suggesting that the current circumscription of the genus is incorrect. There are five instances of this nature described in the discussion which indicate that either a drastic generic realignment is necessary to accommodate this variation or that all these associated taxa should be incorporated into a drastically altered concept of *Pentaschistis*.

The list below shows the placing of all taxa in both the morphological and the anatomical groups.

Species number & name	Morphological group	Anatomical group
1 <i>P. veneta</i>	1A	Ab,Ad
2a <i>P. barbata</i> subsp. <i>barbata</i>		Ab,Ad,Ae
2b <i>P. barbata</i> subsp. <i>orientalis</i>		Bb
3 <i>P. aspera</i>		Bc
4 <i>P. papillosa</i>		Be
5 <i>P. rupestris</i>		Ae
6 <i>P. longipes</i>		Bc
7 <i>P. pallida</i> form A	1B	Aa
7 <i>P. pallida</i> form B		Aa,Ab,Ca
7 <i>P. pallida</i> form C		Be
7 <i>P. pallida</i> form D		Bb
7 <i>P. pallida</i> form E		Bd
7 <i>P. pallida</i> form F		Aa,Ab,Ac,Ad,Ae
7 <i>P. pallida</i> form G		Bb
8 <i>P. densifolia</i>		Ab
9 <i>P. cirrhulosa</i>		Ca,Ec
10 <i>P. tomentella</i>		Ac,Ad
11 <i>P. lima</i>		Ca

12 <i>P. patula</i> form A	1C	Aa
12 <i>P. patula</i> form B		G*
12 <i>P. patula</i> form C		Ab
13a <i>P. airoides</i> subsp. <i>airoides</i>		Ac
13b <i>P. airoides</i> subsp. <i>jugorum</i>		Bd
14 <i>P. capillaris</i>		Ac
15 <i>P. aristifolia</i>		Aa
16 <i>P. trisetoides</i>		G*
17 <i>P. galpinii</i>	1D	Bd
18 <i>P. microphylla</i>	1E	Bd
19 <i>P. ecklonii</i>		Be
20 <i>P. reflexa</i>	1F	Be
21 <i>P. borussica</i>		Bb
22 <i>P. natalensis</i>		Bb
23 <i>P. oreodoxa</i>		Bd
24 <i>P. setifolia</i>		Bd
25 <i>P. ampla</i>		Bb
26 <i>P. glandulosa</i>		Bd
27 <i>P. minor</i>	1G	G*
28 <i>P. mamii</i>		G*
29 <i>P. imatongensis</i>		G*
30 <i>P. pictigluma</i>		G*
31 <i>P. gracilis</i>		G*
32 <i>P. aristidoides</i>	2A	Ca
33 <i>P. velutina</i>		Ca
34 <i>P. viscidula</i>		D
35 <i>P. argentea</i>		D
36 <i>P. trisetia</i>	2B	Ba
37a <i>P. rosea</i>		Ba
subsp. <i>rosea</i>		Ba
37b subsp. <i>purpurascens</i>		Ba
38 <i>P. pseudopallescens</i>		Ba
39 <i>P. pallescens</i>		Ba
40a <i>P. aurea</i> subsp. <i>aurea</i>		Bb
40b <i>P. aurea</i> subsp. <i>pilosogluma</i>		Bb
41 <i>P. colorata</i>	3A	Ea
42 <i>P. tortuosa</i>		Ea
43 <i>P. alticola</i>		Ea
44 <i>P. pyrophila</i>		Fb
45a <i>P. calcicola</i> var. <i>calcicola</i>		Ec
45b <i>P. calcicola</i> var. <i>hirsuta</i>		Ec
46 <i>P. montana</i>	3B	Ca
47 <i>P. rigidissima</i>		Cb
48 <i>P. malouinensis</i>		Ea
49 <i>P. pusilla</i>		Ea,G
50 <i>P. elegans</i>		Ea
51 <i>P. tysonii</i>	3B	Eb
52 <i>P. holciformis</i>		Eb
53 <i>P. chippindalliae</i>		Cb
54 <i>P. exserta</i>		Cb
55 <i>P. basutorum</i>		Cb
56 <i>P. praecox</i>		Eb

Species number & name	Morphological group	Anatomical group
57 <i>P. curvifolia</i>	4	Fa
58 <i>P. pungens</i>		Fa
59 <i>P. acinosa</i>		Fa
60 <i>P. caulescens</i>		Fa
61 <i>P. scandens</i>		Fa
62 <i>P. capensis</i>	5	G
63 <i>P. insularis</i>		G*
64 <i>P. andringitrensis</i>		G*
65 <i>P. humbertii</i>		G*
66 <i>P. chrysurus</i>	6	G*
67 <i>P. heptamera</i>		Be
68 <i>P. eriostoma</i>		Fb

* not studied anatomically, i.e. unplaced species.

The above list clearly shows close congruence at species level between the morphological and anatomical evidence. This suggests that present species delimitation in *Pentascistis* reflects natural taxa. Only in seven taxa were specimens allocated to more than a single anatomical grouping. These are *P. veneta*, *P. barbata* subsp. *barbata* (in which three anatomical forms were recognizable), *P. pallida* forms B and F, *P. tomentella* and *P. pusilla*. The two subspecies of both *P. airoides* and *P. barbata* are also not supported by the anatomy as in both cases the subspecies are placed in different anatomical subgroups. The informal forms recognized in both *P. pallida* and *P. patula* are also not confirmed by the anatomical evidence.

With the exception of *P. pusilla* all of these taxa belong to the glandular species group (Group 1) which is discussed further below.

It is striking that, apart from *P. pallida* form B and *P. pusilla*, all these problem taxa are centred on the Olifants River area at the boundary of the Fynbos and Succulent Karoo Biomes and usually on granitic soils which are at the northern end of the Cape Granite Suite and well separated from the Little Namaqualand Granites which begin north of Vanrhynsdorp. This area of sympatry of all these taxa needs further detailed biosystematic study as hybridization may be the cause of this confusing and conflicting taxonomic pattern.

The current circumscription of *P. pallida*, which exhibits complex morphological variation patterns, is not supported by the anatomical evidence. Specimens of both forms B and F fall into three and five anatomical subgroups respectively and do not represent coherent anatomical entities as presently constituted. In addition the seven informal forms recognized in *P. pallida* also fall into three anatomical species groups (Groups A, B and C) and seven different subgroups. This species undoubtedly presents the greatest taxonomic difficulty in the entire genus.

A comparison of the composition of the different morphologically and anatomically based sections also show the following:

Group	Includes anatomical groups	Includes subgroups
1a	2	6
1b	4	10
1c	2	4
1d	1	1
1e	1	1
1f	1	2
1g	not studied anatomically	
2a	2	2
2b	1	2
3a	3	5
3b	2	3
4	1	1
5	ungrouped or insufficiently studied anatomically	
6	3	3

From this summary it is clear that Group 1b includes the greatest anatomical heterogeneity. This group contains the very variable *P. pallida*, but, even with this species removed, no two species share the same anatomical grouping, which suggests that this group is unnatural. Other Group 1 subgroups similarly lack anatomical cohesion, particularly Group 1a and 1c. This confirms that the glandular *Pentascistis* species present taxonomic problems.

The other morphological species groups are mostly supported by the anatomical evidence and the differences in composition are largely due to further subdivision based on anatomical information. Nevertheless, a core group of species is usually common to both groupings, illustrating the complementary aspects of these two data sets.

In the species with mesic anatomy and stalked multicellular glands, species delimitations and groupings based on morphological evidence are not supported by anatomical data. All the other species (with mesic anatomy but with glands lacking collar and subglandular cells or with sclerophyllous anatomy) show very close congruence between the anatomy and the morphology. A possible cause of this discrepancy may be that anatomical features were subdivided too finely—particularly the classification of the different gland types. Different interpretations of gland types has resulted in many of these differences in delimitation of species and species groups. This undue reliance on a single character (in both data sets) is unsatisfactory and a probable cause of this variance.

Any future systematic studies of *Pentascistis* must necessarily take these anatomical indications into account. It will also be meaningless to study *Pentascistis* in isolation from neighbouring arundinoid genera and such studies will have to synthesise as many different character sets as possible from all these arundinoid taxa in order to satisfactorily delimit meaningful genera.

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FIGURES

FIGURE 1.1.—*Pentaschistis veneta*: transectional leaf anatomy showing gradation from expanded, thin and soft leaves to narrower, inrolled leaves with well-developed supporting tissue.

A, wide, flat, thin mesic leaf with little sclerenchyma and very diffuse mesophyll; note cushion bases of macrohairs (arrowed).

B, detail of blade margin showing longitudinally sectioned stalked gland (arrowed); note wide bulliform cell groups.

C, marginal, stalked, multicellular gland (arrowed) showing gland and stalk cells.

D, lateral part of lamina with macrohair and cushion base cells in section (arrowed); note diffuse nature of mesophyll and small strands and girders of fibres associated with the vascular bundles.

E, marginal, stalked gland (arrowed); note ribbing more prominent with bulliform groups restricted to fans at bases of furrows.

F, detail of marginal gland and well-developed adaxial and abaxial sclerenchyma girders imparting rigidity to the blade.

G, expanded leaf transection but thickness considerably greater than that of the soft, thin leaf of A.

H, marginal gland (arrowed); note small size of bulliform cells.

I, narrow, inrolled leaf outline with marginal gland (arrowed) visible.

J, detail of this thickened, strengthened leaf showing supporting sclerenchyma girders associated with all the vascular bundles; note adaxially located multicellular gland (arrowed) located costally above the penultimate bundle; this gland is dome-like and not clavate.

A, B, D, *Ellis* 5596; C, *Ellis* 5594; E, F, *Linder* 4601; G, H, *Ellis* 5490; I, J, *Ellis* 5595. A, G, I, $\times 100$; E, $\times 160$; B, C, D, F, H, J, $\times 250$.

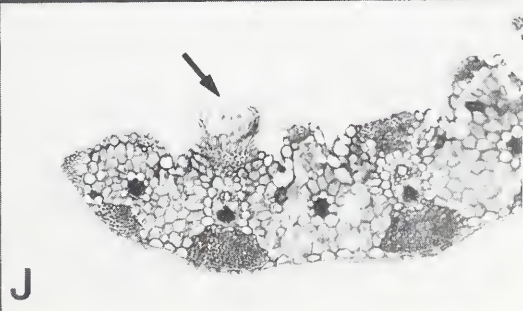
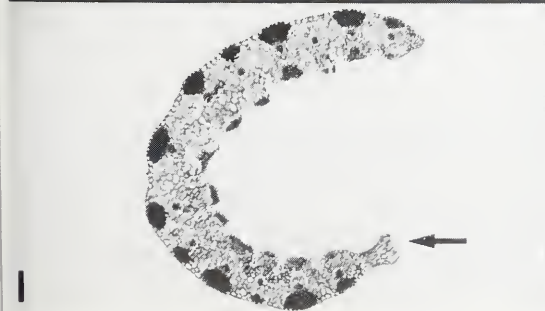
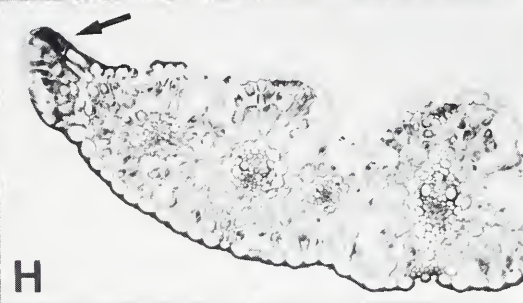
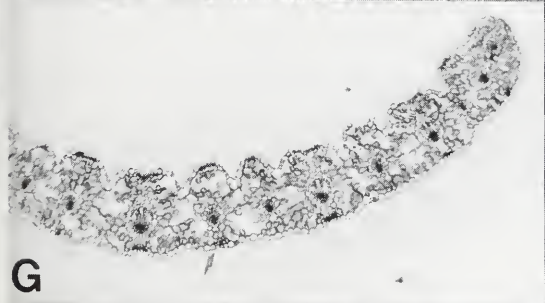
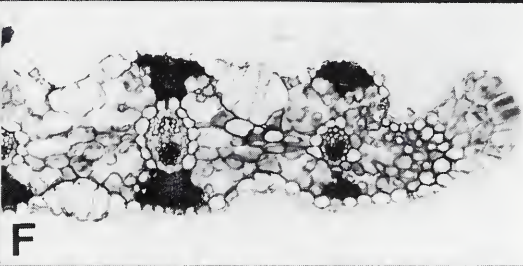
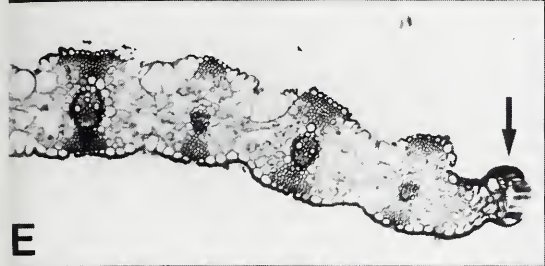
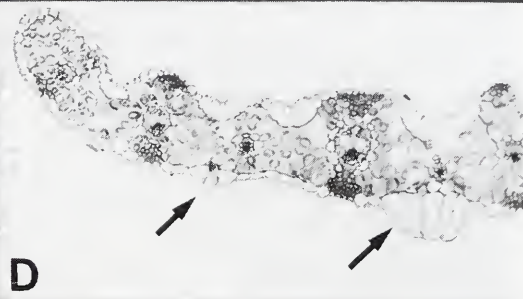
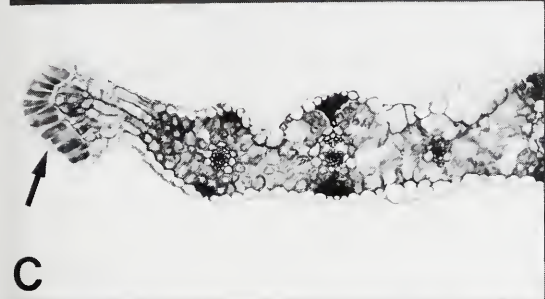


FIGURE 1.2.—*Pentaschistis veneta*: abaxial epidermis illustrating the same variation sequence as in the transverse sections (Figure 1.1) i.e. from expanded, soft leaves to narrower, tougher leaves.

A, margin of soft, thin leaf showing stalked, multicellular glands and cushion-based macrohairs.

B, detail of constricted macrohair bases sunken between raised cushion cells, microhairs (arrowed) and costal prickles.

C, margin of soft, mesic leaf with stalked glands and clearly defined, but narrow, costal zones.

D, epidermal detail with macrohairs, microhairs and costal and intercostal cell detail.

E, lateral part of blade with raised marginal gland with short stalk and long, stiff, cushion-based macrohairs.

F, detail of macrohairs showing fungal hyphae (arrowed) which are commonly associated with these hairs in this species; also visible are microhairs, stomata and dumbbell-shaped silica bodies.

G, epidermis of the narrow, thicker leaf type illustrated in transection in Figure 1.II & J; note absence of macrohairs and wider costal zones associated with the well-developed sclerenchyma girders; a stalked multicellular gland is visible on the leaf margin.

H, detail of G with elongated intercostal long cells with sinuous anticlinal walls, stomata and microhairs and wide costal zones with dumbbell-shaped silica bodies.

A, B, *Ellis* 5594; C, D, *Linder* 4601; E, F, *Ellis* 5490; G, H, *Ellis* 5595. C, $\times 100$; A, D, E, G, $\times 160$; B, F, H, $\times 250$.

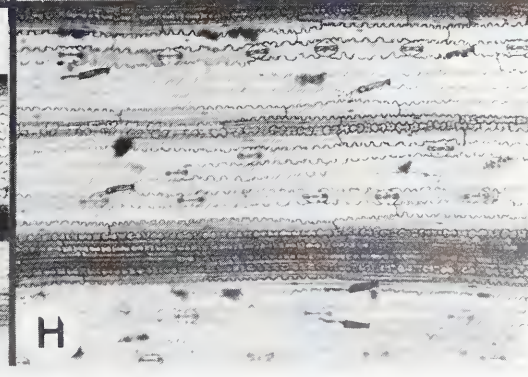
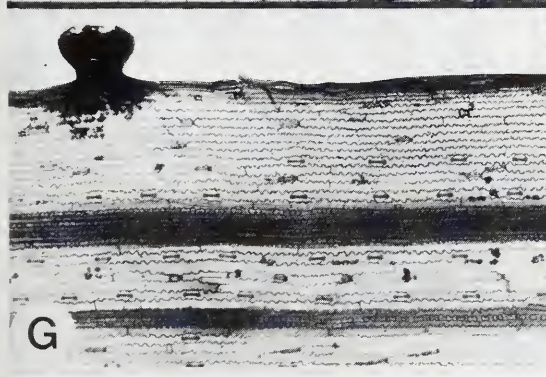
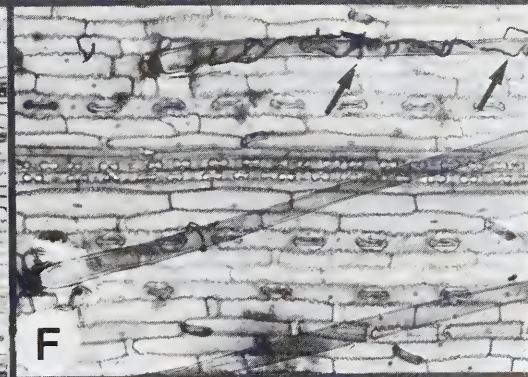
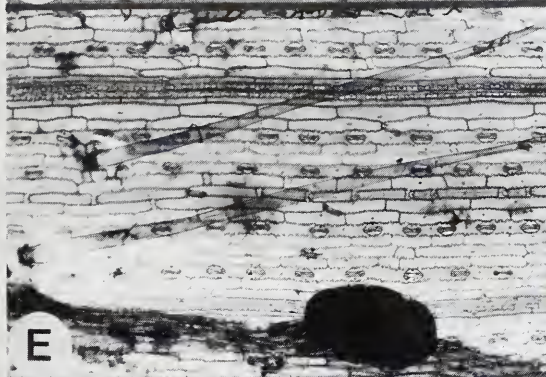
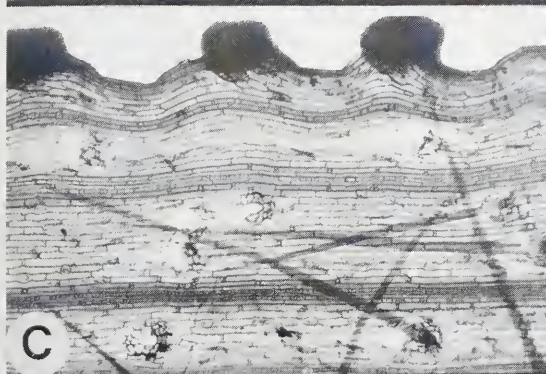
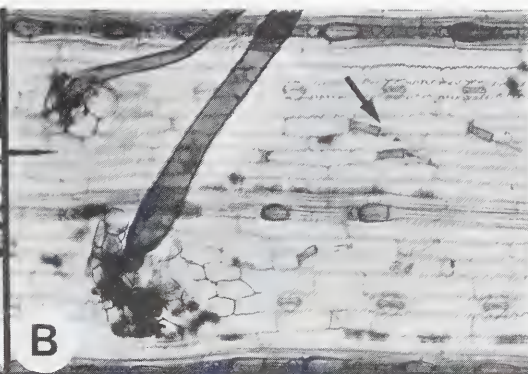
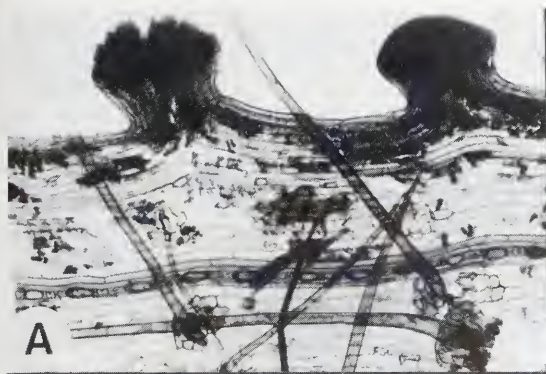


FIGURE 1.3.—*Pentaschistis veneta*: leaf blade ultrastructure, contrasting the expanded, thin, soft leaf type (A–D) with the narrow, thicker, strengthened leaf type (E–H). The two specimens illustrated come from the same population in close proximity to one another. A, B, E, F, abaxial epidermis; C, D, G, H, adaxial epidermis.

A, macrohairs with raised cushion bases; note costal prickles with short barbs.

B, finger-like microhair with distal cell longer than the basal cell.

C, adaxial macrohairs, thinner than those on the abaxial surface, but also with raised cushion bases; costal ribs with numerous small prickles; no adaxial microhairs seen.

D, stalked, clavate, marginal gland with convex apex and elongated stalk cells.

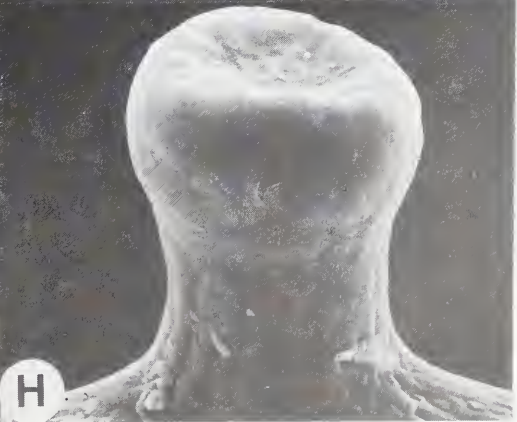
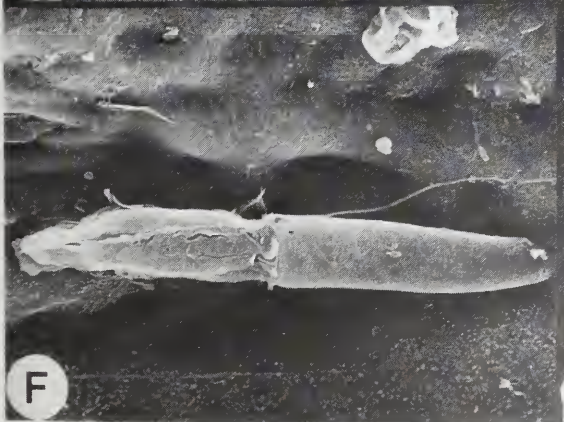
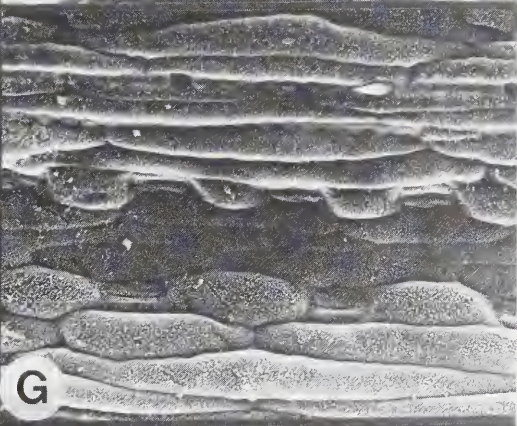
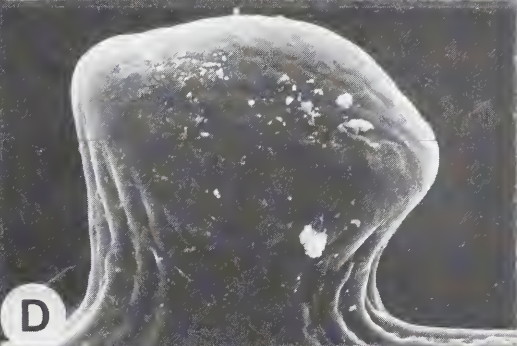
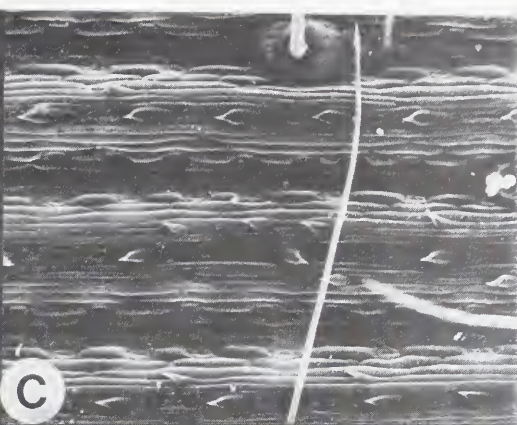
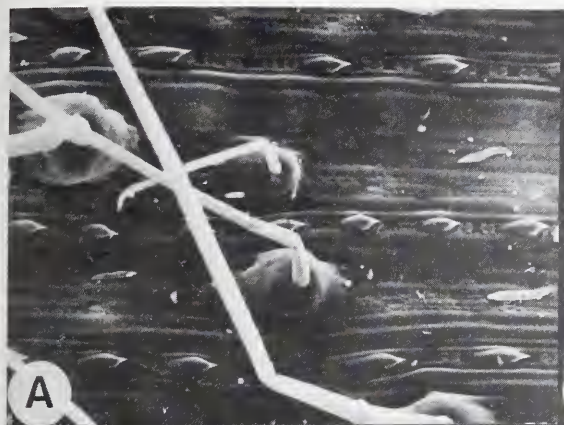
E, short abaxial macrohair without raised cushion base; fusoid intercostal long cells with sinuous, thickened anticlinal walls; costal zone with dumbbell-shaped silica bodies.

F, elongated microhair with basal and distal cells equal in length; hair shorter than those from soft, mesic leaves (Figure 1.3B).

G, no adaxial macrohairs or microhairs; intercostal and interstomatal long cells with inflated periclinal walls which overarch the slightly sunken stomata.

H, stalked, clavate marginal gland with concave apex.

A–D, *Ellis* 5594; E–H, *Ellis* 5595. A, C, $\times 60$; D, E, G, $\times 200$; H, $\times 280$; B, $\times 690$; F, $\times 880$.



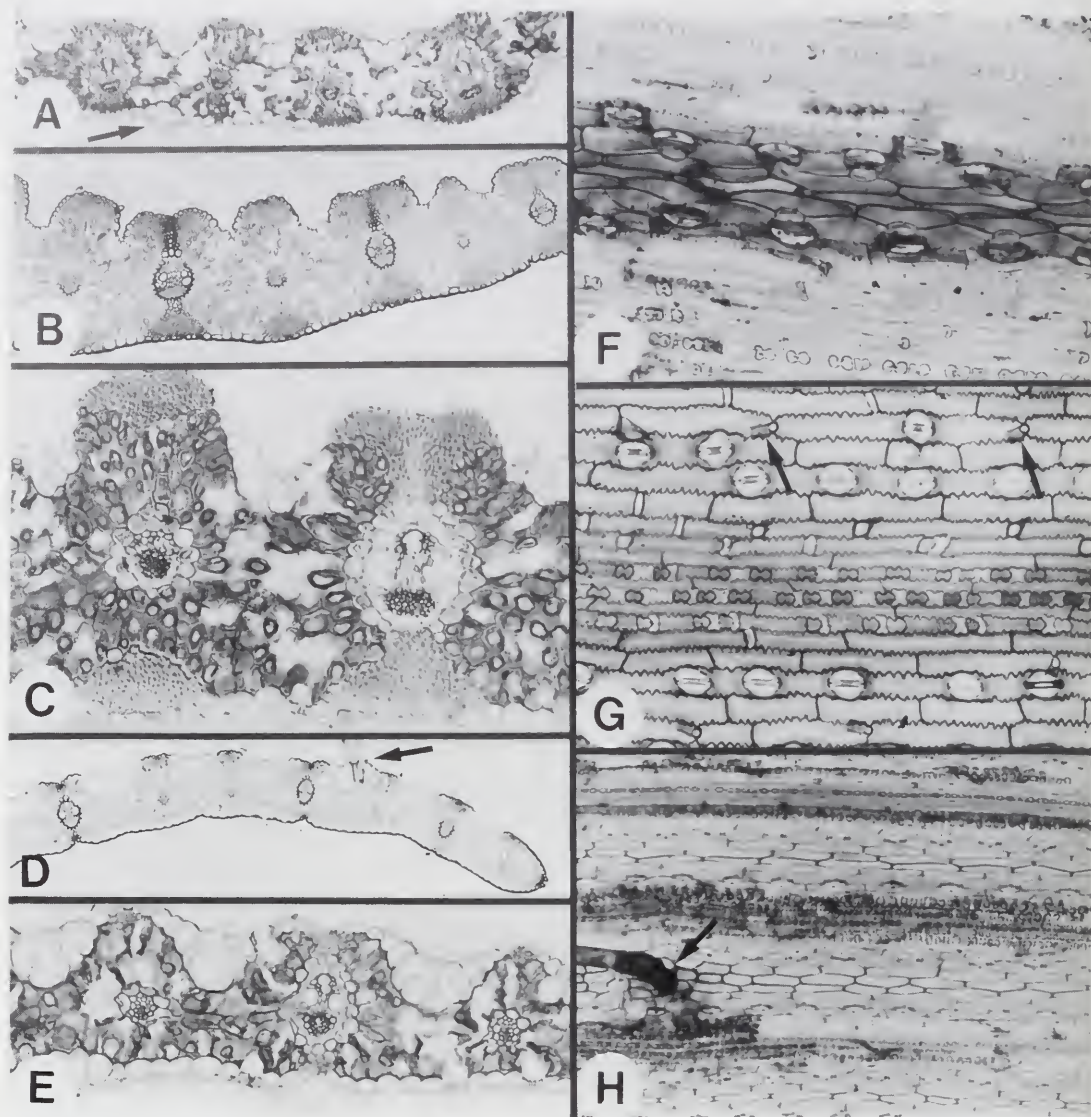


FIGURE 2a.1.—*Pentaschistis barbata* subsp. *barbata*: leaf anatomy of the mesic, montane form. A–E, leaf in transverse section; F–H, abaxial epidermis.

A, expanded, flat leaf with diffuse mesophyll; adaxial ribs and furrows not well developed; sclerenchyma girders not prominent; note cushion base of macrohair (arrowed).

B, expanded, open leaf with ribs, furrows and sclerenchyma better developed.

C, detail of adaxial ribs and furrows and T-shaped girders; abaxial girders trapezoidal; note mesophyll composed of large chlorenchyma cells with extensive intercellular air space system.

D, thin, soft expanded mesic leaf with macrohair cushion base (arrowed).

E, detail of diffuse mesophyll and very shallow adaxial ribs and furrows; small sclerenchyma girders associated with the first order vascular bundles and minute strands with the smaller bundles; bulliform cells well developed in wide, open fans.

F, epidermal zonation showing intercostal zones with stomata, and costal zones with irregularly dumbbell-shaped silica bodies.

G, costal zone with alternating dumbbell-shaped silica bodies and intercostal zones with long cells with sinuous walls, dome-shaped stomata and microhairs (arrowed).

H, epidermal zonation with clear distinction between costal zones and intercostal zones; note base of cushion-based macrohair (arrowed).

A, F, *Ellis* 2219; B, C, G, *Ellis* 2234; D, E, H, *Ellis* 2305. A, B, D, $\times 100$; H, $\times 160$; C, E–G, $\times 250$.

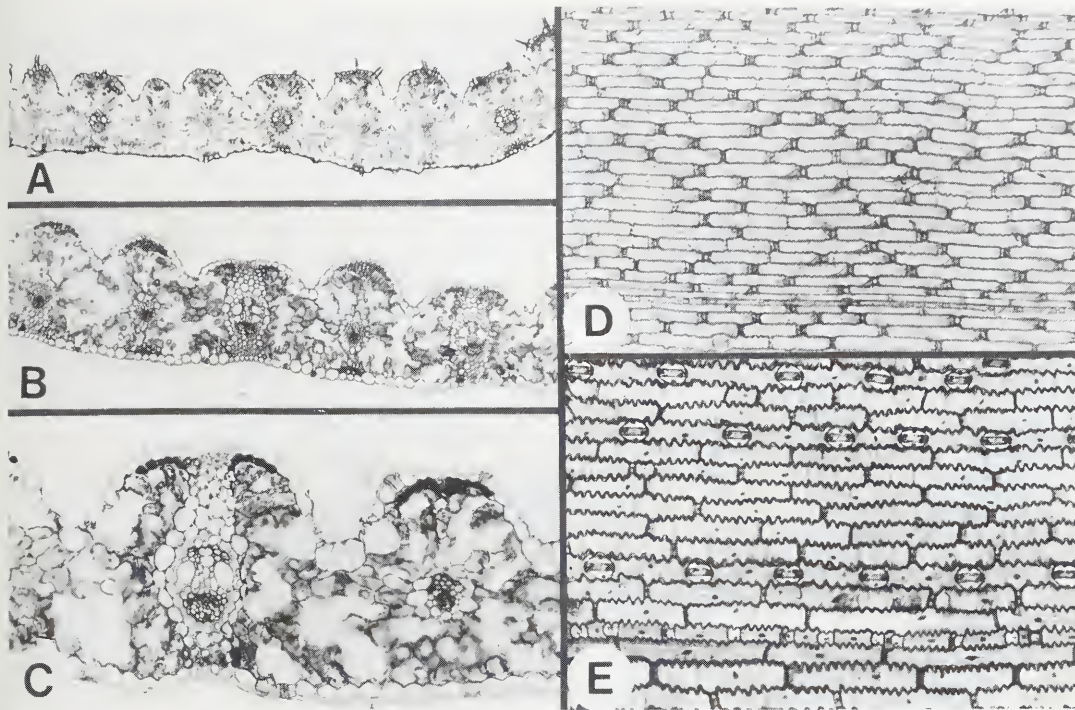


FIGURE 2a.2.—*Pentaschistis barbata* subsp. *barbata*: leaf anatomy of the sandveld form. A–C, leaf in transverse section; D, E, abaxial epidermis.

A, open, expanded outline showing medium adaxial ribs and furrows and minute sclerenchyma strands and girders; note prickles in both epidermides.

B, flat, expanded outline with medium ribs and furrows and small bulliform cells; sclerenchyma girders and strands more prominent than in A.

C, anatomical detail of distinct adaxial ribs and furrows, small girders associated with large vascular bundles and only small adaxial strands with the smaller bundles; note diffuse mesophyll, thick cuticle and adaxial prickles overarching the furrows.

D, abaxial epidermis without stomata and with indistinct zonation; narrow costal zones (3 cells wide) overlie first order vascular bundles only and costal zones are not evident over third order bundles (as indicated by the trans-section in C); note small hooks present between virtually all long cells.

E, abaxial epidermis with stomata and clear zonation; intercostal long cells with moderately sinuous walls and not separated by hooks; narrow costal zone with irregularly dumbbell-shaped silica bodies.

A, Ellis 5136; B, Ellis 5134; C, D, Ellis 5802; E, Ellis 5135. A, B, $\times 100$; D, $\times 160$; C, E, $\times 250$.

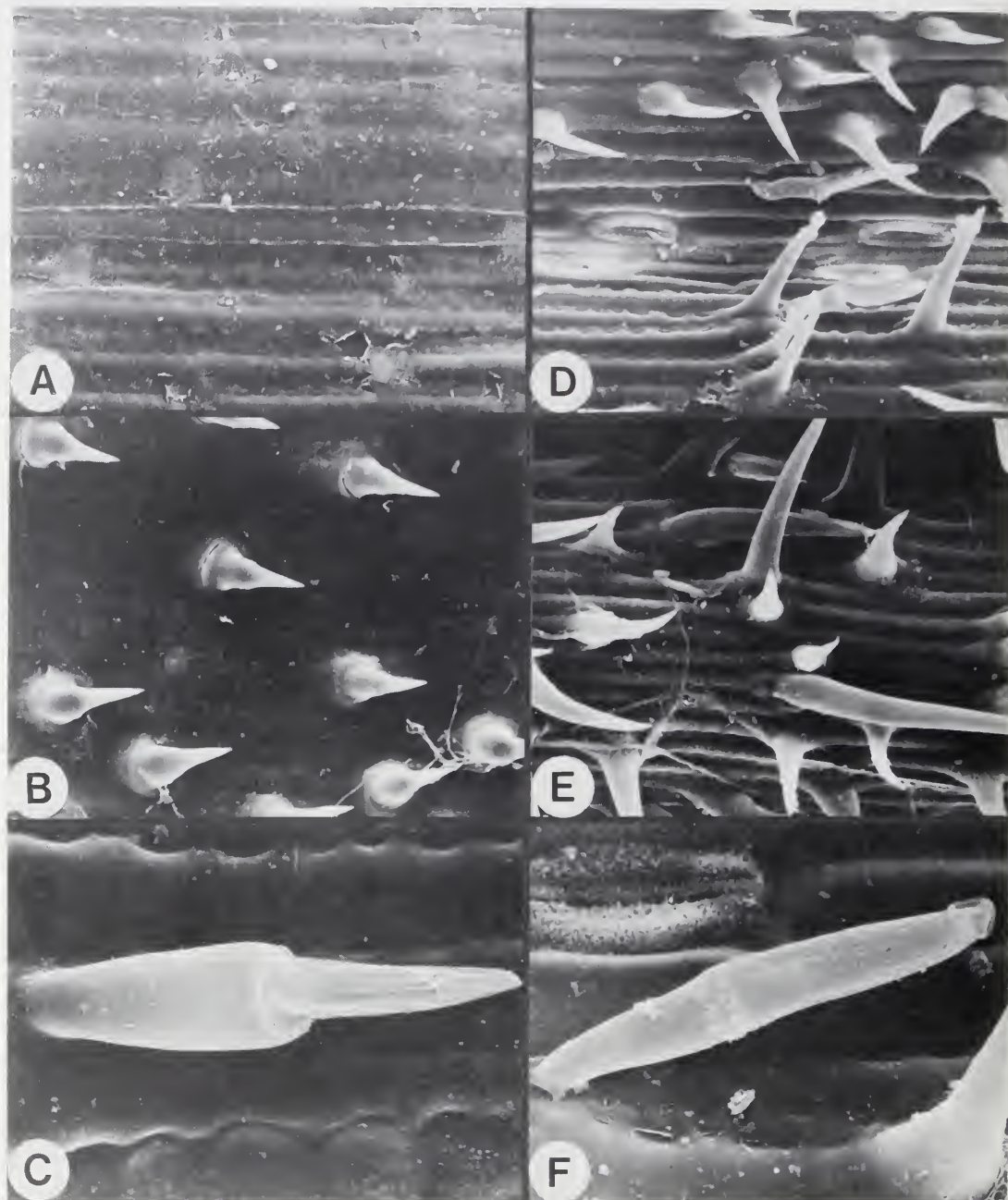


FIGURE 2a.3. — *Pentaschistis barbata* subsp. *barbata*: leaf blade ultrastructure of the sandveld form. A, B, abaxial epidermis; C–F, adaxial epidermis.

A, featureless abaxial epidermis without zonation, stomata or prickles possibly due to thick cuticle; long cells with only slightly undulating anticlinal walls.

B, epidermis without zonation or stomata but small hooks present between long cells.

C, adaxial microhair with the two cells of equal length.

D, costal prickles with long barbs interlocking over stomata and microhairs in adaxial furrow.

E, adaxial costal prickles located on rib; barb length variable, but always longer than the hooks on the abaxial surface as in B.

F, adaxial microhair with basal cell slightly shorter than the distal cell but length of this hair much less than that illustrated in C; note prickles and stoma.

A, D, F, *Ellis 5134*; B, E, *Ellis 5802*; C, *Ellis 5136*. A, B, D, E, $\times 200$; F, $\times 660$; C, $\times 1020$.

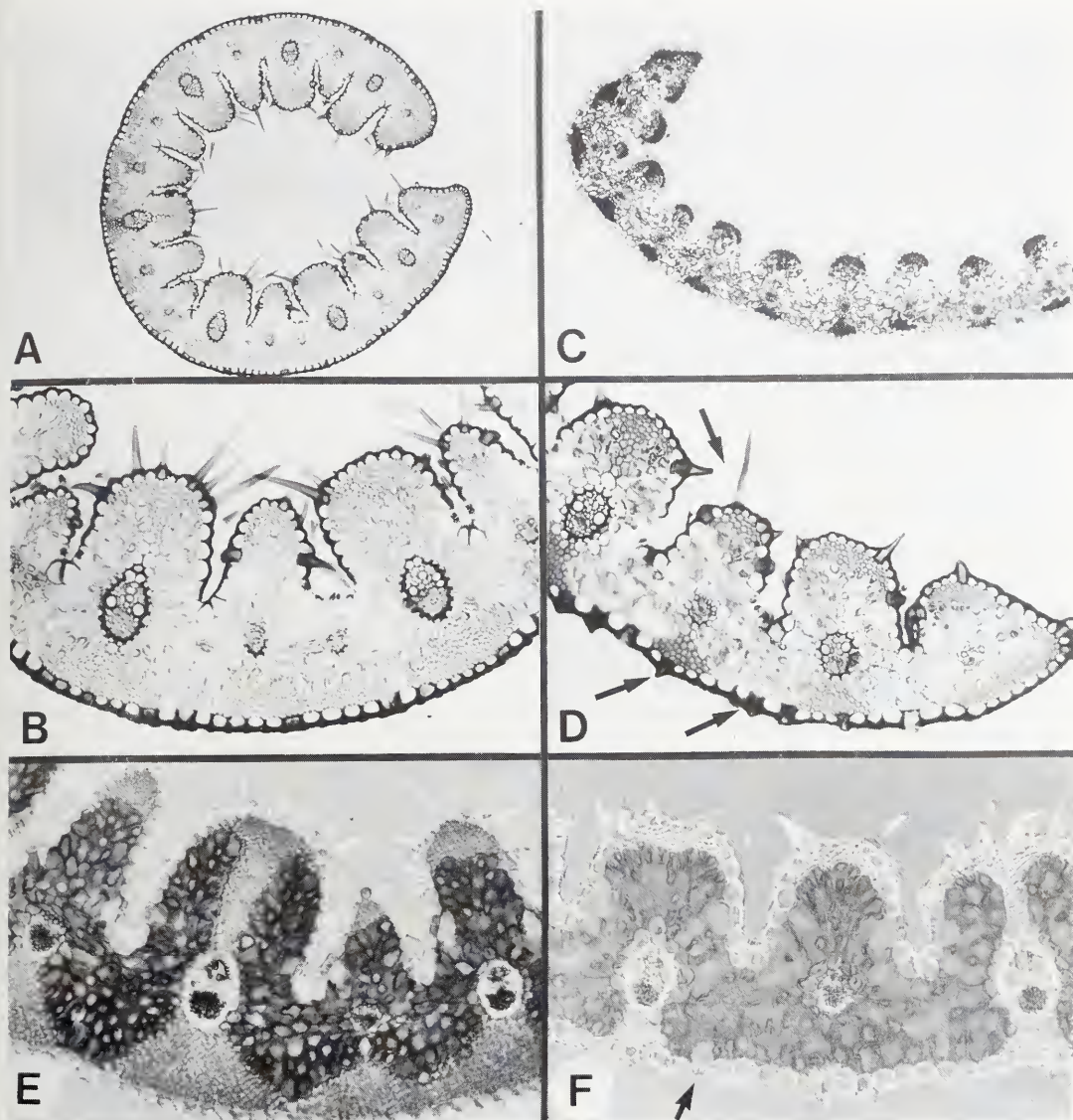


FIGURE 2a.4.—*Pentaschistis barbata* subsp. *barbata*: transectional leaf anatomy of the strandveld form.
 A, narrow, inrolled leaf outline.
 B, detail of massive adaxial ribs and cleft-like furrows with interlocking prickles; abaxial sclerenchyma girders fused to form continuous subepidermal layer.
 C, leaf blade in expanded state but demonstrating inrolling ability.
 D, lateral part of blade with large ribs and deep furrows; note adaxial prickles (arrowed) and abaxial hooks (arrowed).
 E, interference contrast showing fused abaxial girders; note diffuse nature of mesophyll cells.
 F, interference contrast of specimen without hypodermal layer; sclerenchyma girders poorly developed but epidermis, nevertheless, without zonation although a few stomata are visible in section (arrowed).
 A, B, *Ellis* 2360; C, D, *Ellis* 5804; E, *Ellis* 2359; F, *Ellis* 1684. A, C, $\times 100$; B, D–F, $\times 250$.

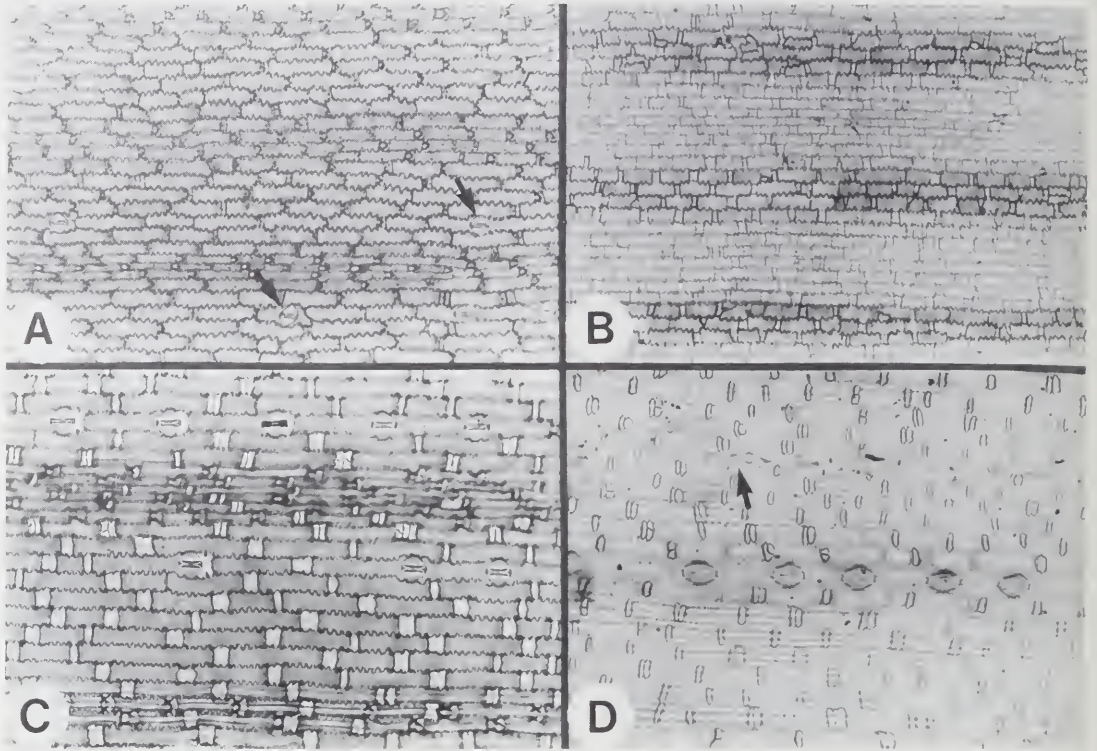


FIGURE 2a.5.—*Pentaschistis barbata* subsp. *barbata*: abaxial epidermis of the strandveld form.

- A, costal and intercostal zones barely distinguishable and all long cells of similar length and width; costal zones distinguishable due to presence of underlying fibres; note few, scattered stomata (arrowed).
 B, zonation barely evident with intercostal zones staining slightly darker but, structurally the cells are very similar to the costal long and short cells; no stomata present.
 C, narrow costal zones with small hooks and wide intercostal zones with few stomata in restricted cell files; note all intercostal long cells interspaced by paired short cells and not hooks.
 D, single file of stomata in centre of narrow intercostal zone; costal long cells separated by paired short cells with narrow files of hooks in centre of zone (arrowed); no dumbbell silica bodies.

A, Ellis 5804; B, Ellis 2359; C, Ellis 1684; D, Ellis 2360. A, B, $\times 160$; C, D, $\times 250$.

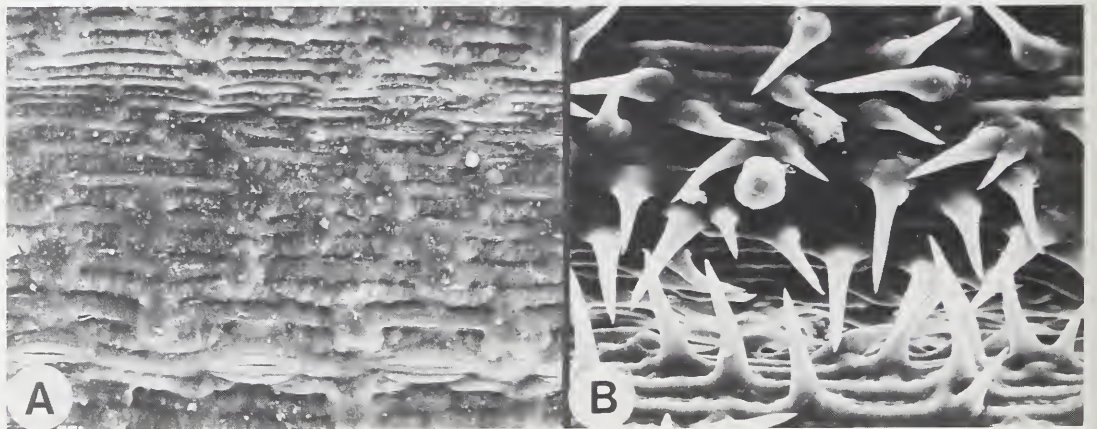


FIGURE 2a.6.—*Pentaschistis barbata* subsp. *barbata*: ultrastructure of the strandveld form.

- A, abaxial epidermis showing absence of differentiation between costal and intercostal zones; an isolated file of stomata is visible at the bottom of the picture.

B, adaxial epidermis with interlocking prickles overlying a cleft-like adaxial groove.

A, B, Ellis 5803. A, B, $\times 210$.

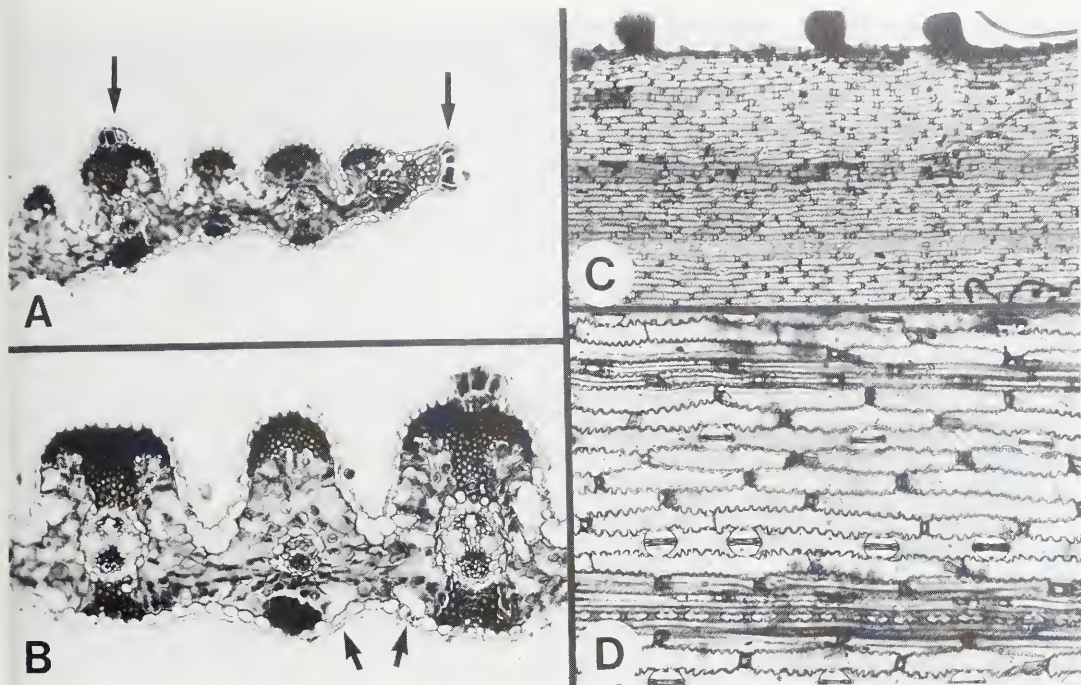


FIGURE 2a.7.—*Pentaschistis barbata* subsp. *barbata*: leaf blade anatomy of the northern strandveld form. A, B, leaf in transverse section; C, D, abaxial epidermis.

A, section of lateral part of leaf showing marginal and adaxial glands (arrowed).

B, detail of deep, narrow furrows and massive ribs with anchor-shaped adaxial girders; abaxial girders not as well developed; note adaxial prickles and gland situated above the ribs; mesophyll is diffuse and abaxial stomata are visible in section (arrowed).

C, epidermis showing lateral glands and poorly defined zonation.

D, epidermal detail with intercostal stomata, hooks and microhairs; costal zones narrow with irregularly dumbbell-shaped silica bodies.

A–C, *Ellis 5801*; D, *Ellis 5132*. A, C, $\times 160$; B, D, $\times 250$.

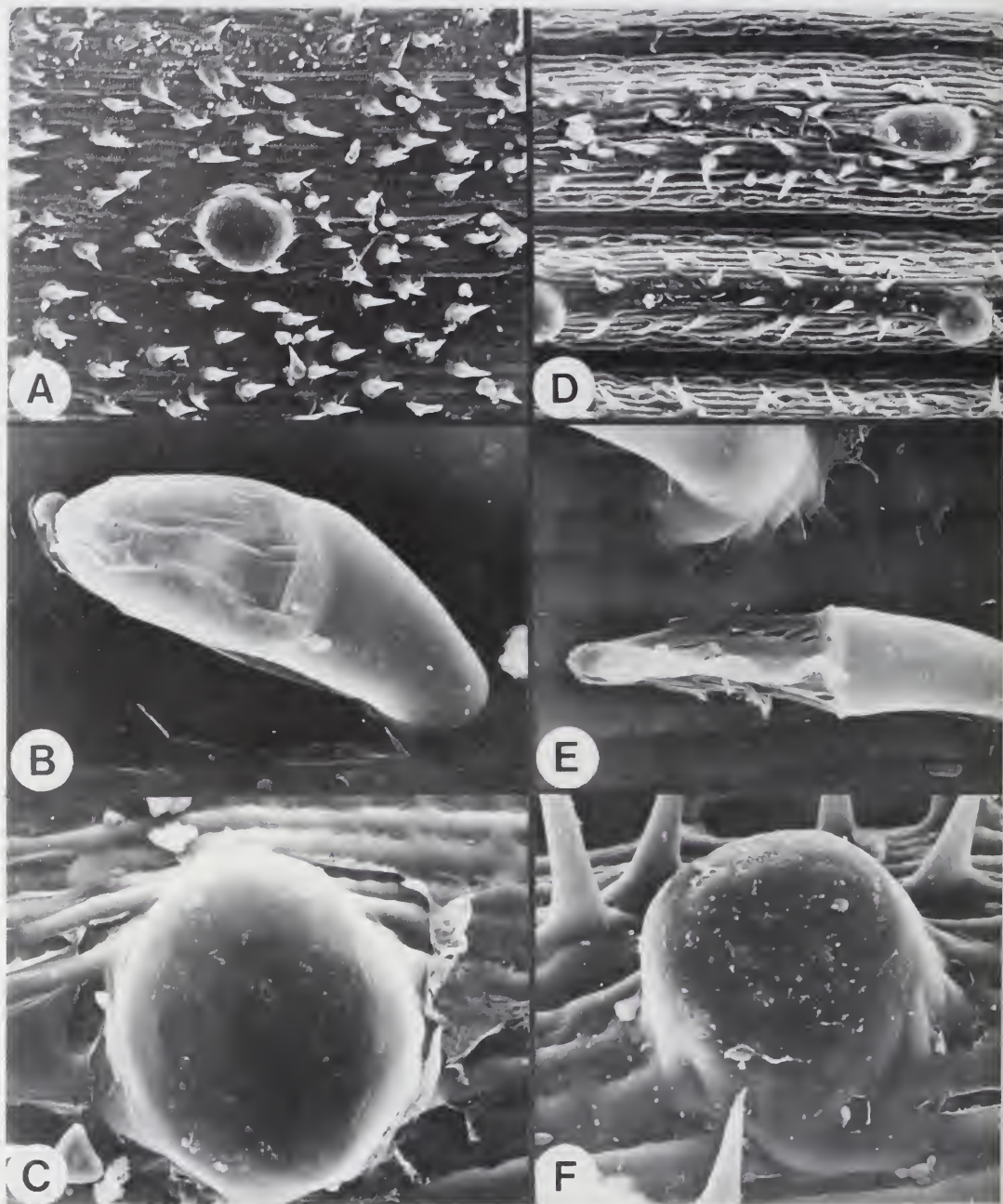


FIGURE 2a.8.—*Pentaschistis barbata* subsp. *barbata*: scanning electron microscopy of both epidermides of the northern strandveld form. A–C, abaxial epidermis; D–F, adaxial epidermis.

A, uniform unzoned epidermis with many small hooks and a single, abaxial, domed gland.

B, short, rather inflated microhair with both cells of equal length.

C, detail of abaxial gland with smooth, convex surface on which cell outlines are not visible.

D, raised glands and prickles on adaxial ribs separated by deep furrows with stomata.

E, elongated adaxial microhair.

F, adaxial dome-shaped gland located on rib between adaxial prickles; note convex shape and absence of cell outlines. A–D, *Ellis* 580I; E, F, *Ellis* 5132. A, D, $\times 60$; C, $\times 340$; F, $\times 360$; E, $\times 800$; B, $\times 900$.

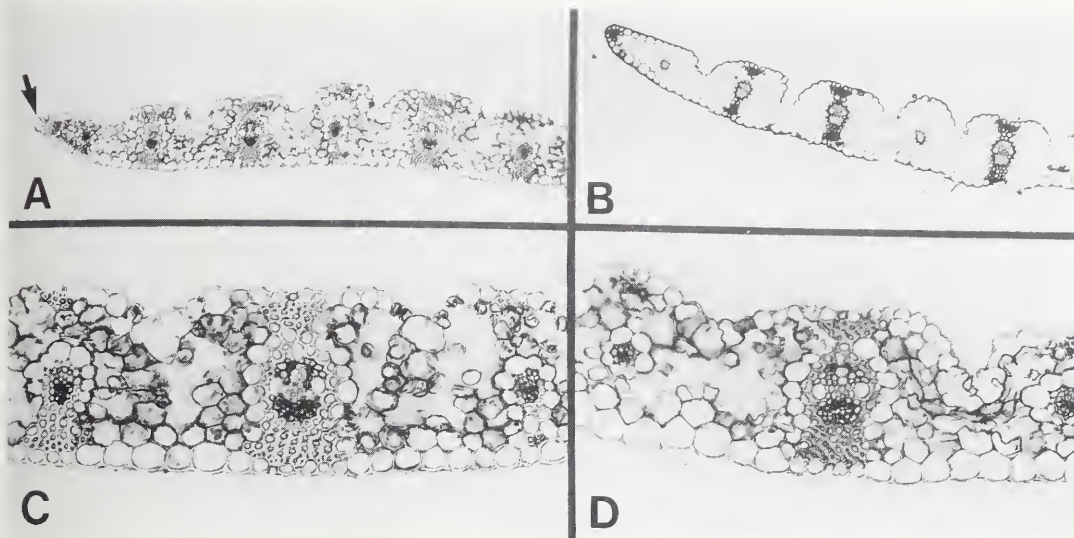


FIGURE 2b.1.—*Pentaschistis barbata* subsp. *orientalis*: transsectional leaf anatomy.

A, tapering leaf margin with small gland in section (arrowed).

B, lateral part of blade showing adaxial ribs and furrows and alternating first and third order vascular bundles.

C, detail of very diffuse mesophyll tissue with large intercellular air spaces; sclerenchyma girders associated with all vascular bundles; adaxial and abaxial girders with first order bundles but third order bundles only with abaxial girders.

D, typical mesic transsectional anatomy.

A, C, Ellis 6002; B, D, Linder 5049. A, B, $\times 100$; C, D, $\times 250$.

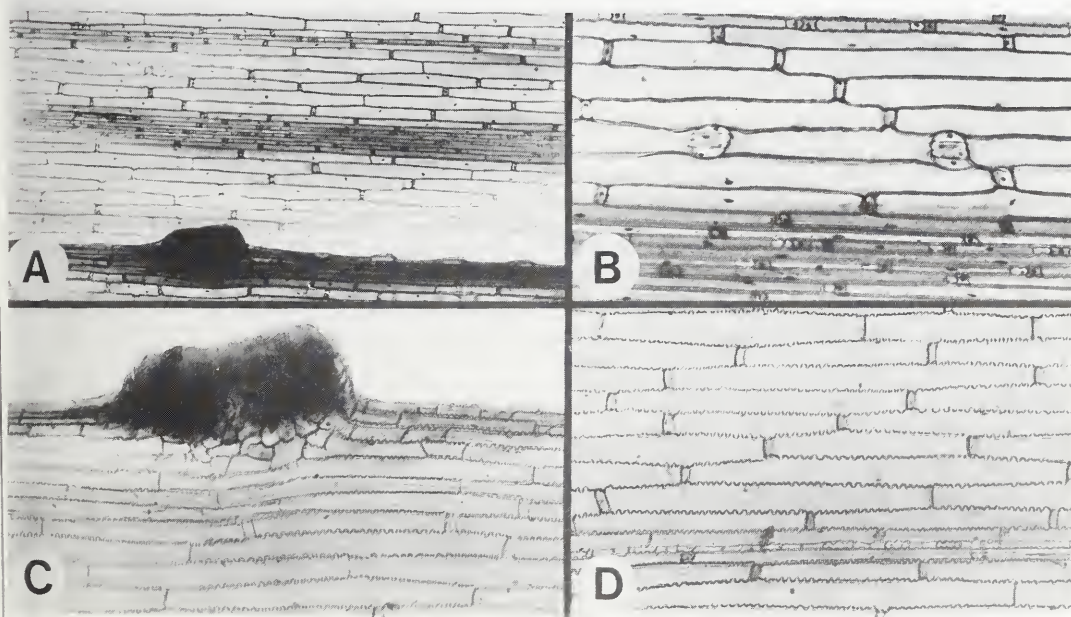


FIGURE 2b.2.—*Pentaschistis barbata* subsp. *orientalis*: abaxial epidermal structure.

A, marginal gland, distinguishable intercostal and costal zones and very few stomata.

B, cell detail showing very elongate intercostal long cells without sinuous walls, narrower costal long cells and very few stomata; no microhairs evident.

C, detail of short-stalked marginal gland resembling the wrap-around type of *P. aspera*.

D, long cells with slightly sinuous walls all alternating with single intercostal short cell; costal cells very narrow and silica bodies are of the nodular type.

A, B, Ellis 6002; C, D, Linder 5049. A, $\times 100$; B–D, $\times 250$.

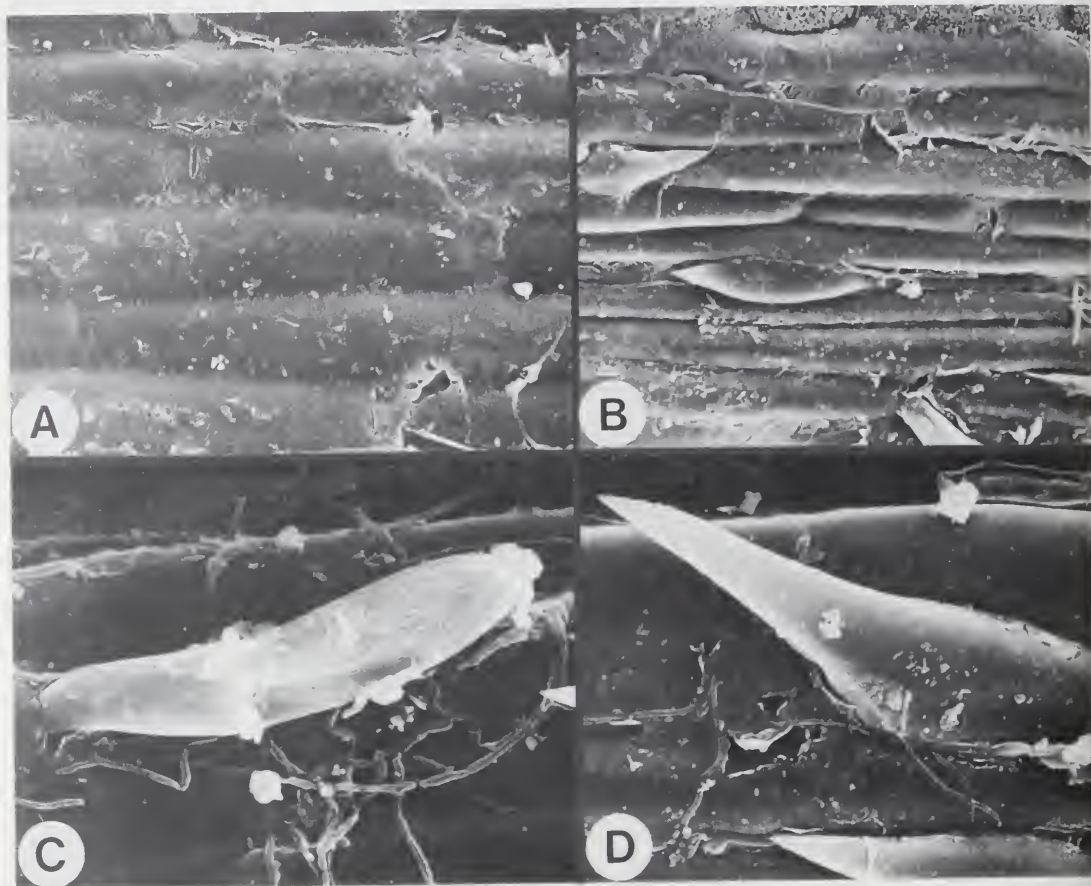


FIGURE 2b.3.—*Pentaschistis barbata* subsp. *orientalis*: epidermal ultrastructure. A, abaxial epidermis. B–D, adaxial epidermis.

A, featureless surface structure with large, elongated intercostal long cells without sinuous walls; no epidermal appendages.

B, short-barbed prickles on slight adaxial ribs.

C, microhair with blunt distal cell which is longer than the basal cell.

D, detail of prickles.

A–D, *Ellis 6002*. A, B, $\times 200$; C, D, $\times 460$.

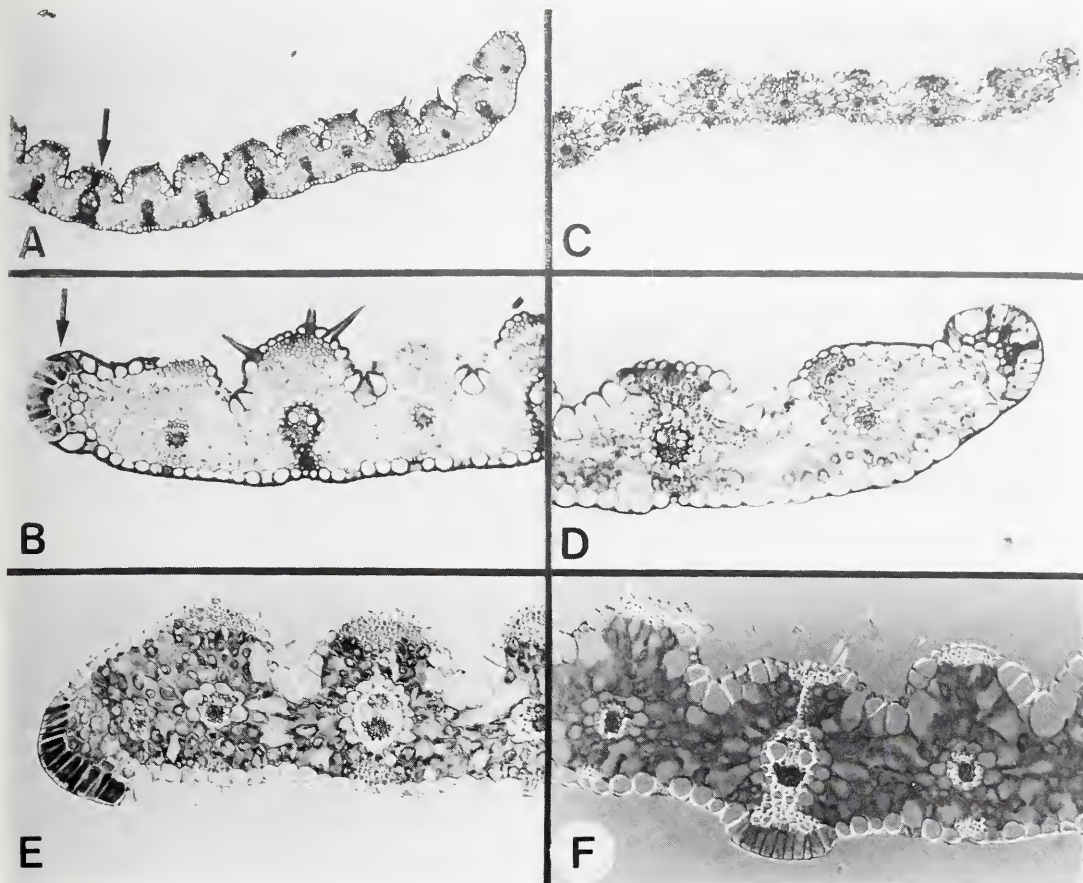


FIGURE 3.1.—*Pentaschistis aspera*: transectional leaf blade anatomy.

A, outline of one half of lamina showing expanded nature of the blade, the median vascular bundle (arrowed), medium adaxial ribs and furrows and margin not tapering; this outline is typical of this species.

B, detail of leaf margin showing wrap-around saddle type of marginal multicellular gland (arrowed) in which the stalk cells are not elongated; note adaxial prickles of the interlocking type with long barbs.

C, anatomy of an atypical specimen with softer, more mesic anatomy in which the ribs are small with open, shallow furrows; leaf blade is thinner than is usual for this species.

D, detail of soft, mesic leaf showing saddle-like marginal gland.

E, interference contrast of saddle-like marginal gland showing darkly stained glandular cells and unstained collar cells; note diffuse, mesic type of chlorenchyma and rounded ribs and medium furrows.

F, interference contrast of unstalked abaxial gland located in costal zone beneath first order vascular bundle.

A, B, *Ellis* 5437; C, D, *Ellis* 5540; E, *Ellis* 679; F, *Ellis* 2328. A, C, $\times 100$; B, D–F, $\times 250$.

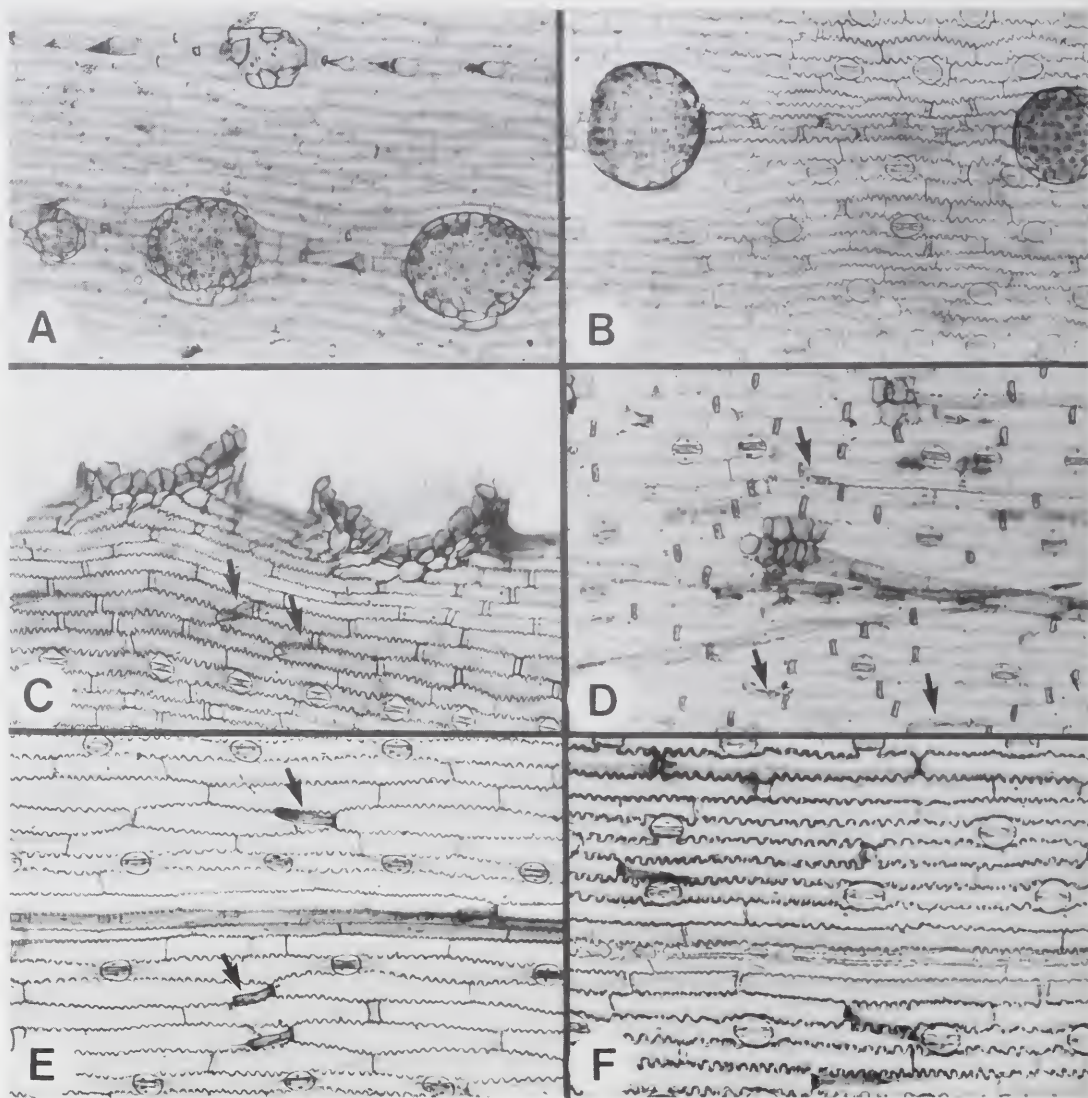


FIGURE 3.2.—*Pentaschistis aspera*: abaxial epidermal structure.

- A, round, unstalked multicellular glands located in files along the costal zones i.e. immediately below the vascular bundles; note nucleate glandular cells surrounded by collar cells; small prickles are also present along the costal zones.
- B, costal multicellular glands showing isodiametric anticlinal walls of the glandular cells; note sinuous walls of intercostal long cells and dome-shaped stomatal subsidiary cells.
- C, detail of wrap-around marginal glands showing clear distinction between glandular and collar cells; note microhairs (arrowed) and stomata.
- D, uncommon macrohairs in which the hair base is swollen and superficial but surrounded by several modified epidermal cells; tall and narrow short cells separate all intercostal long cells; stomata and microhairs (arrowed) are visible.
- E, epidermis of soft, mesic-leaved specimen in which the long cells are much larger and more elongated than in the usual leaf type; note stomata, short cells and microhairs (arrowed).
- F, typical more rigid leaf showing thicker more sinuous long cell walls, the cells being much shorter and narrower than the soft mesic leaf of E, which is less magnified; note dome-shaped subsidiary cells and very elongated microhairs.

A, Ellis 2328; B, Ellis 2323; C, D, Ellis 2337; E, Ellis 5540; F, Ellis 5575. A–E, $\times 250$; F, $\times 400$.

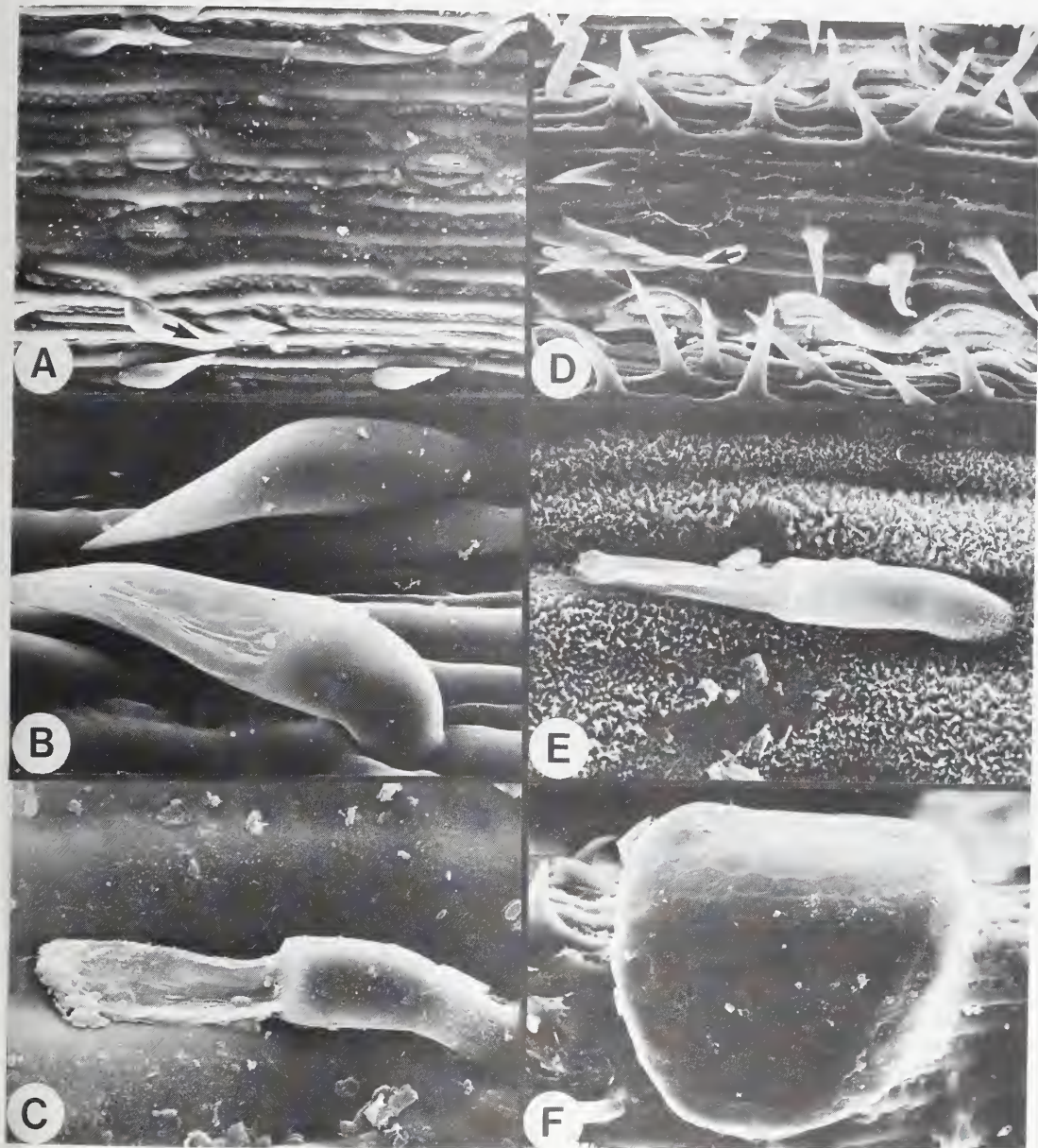


FIGURE 3.3.—*Pentaschistis aspera*: scanning electron microscopy of the upper and lower epidermides. A–C, abaxial epidermis; D–F, adaxial epidermis.

A, intercostal zone with stomata and thick-walled, sinuous long cells; narrow costal zone with small prickles; note microhair (arrowed) which is enlarged in B.

B, tapering abaxial microhair in which the distal cell is longer than the basal cell; note costal prickle with short, sharp barb.

C, finger-like abaxial microhair with distal cell truncated and not tapering; cells of equal length.

D, adaxial rib with interlocking costal prickles with long barbs; note microhair (arrowed) and stomata located at the base of the furrows.

E, elongated adaxial microhair, narrower than the abaxial hairs, but both cells of similar length.

F, wrap-around, saddle-like marginal gland.

A, B, D, F, *Ellis* 5437; C, *Ellis* 5540; E, *Ellis* 5575. A, D, F, $\times 200$; C, $\times 700$; B, E, $\times 800$.

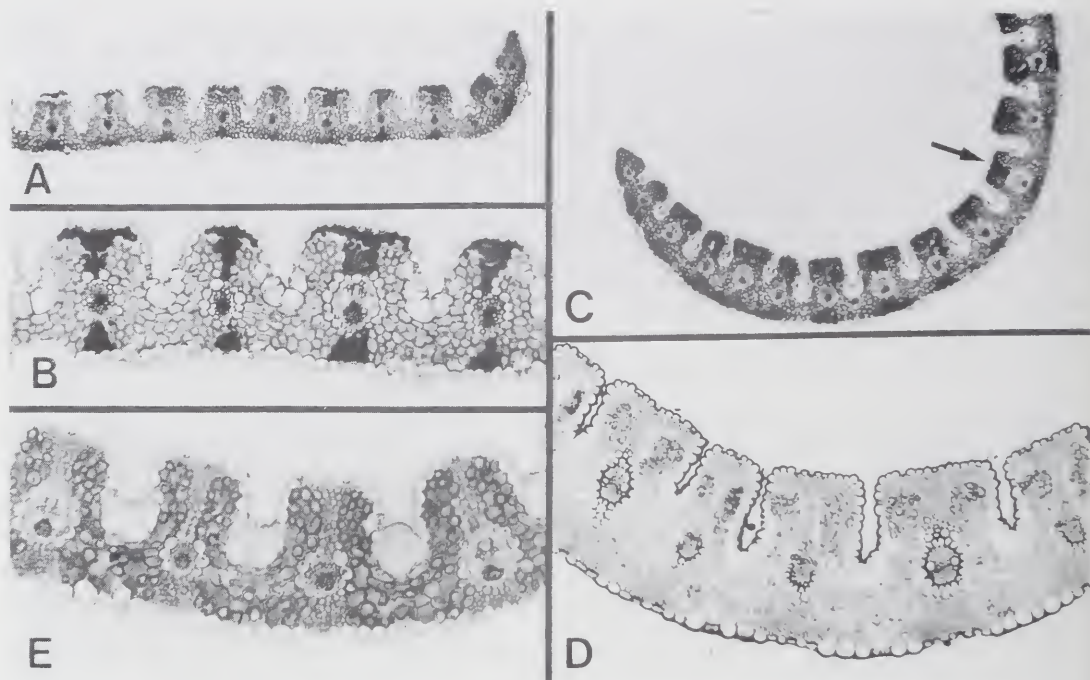


FIGURE 4.1.—*Pentaschistis papillosa*: leaf anatomy as seen in transverse section.

A, expanded, open outline with margin slightly tapering.

B, anatomical detail with large, flat-topped ribs and deep furrows over all vascular bundles; all bundles with adaxial anchor-shaped girders and abaxial girders small and equidimensional.

C, inrolled leaf outline with uniform flat-topped adaxial ribs and deep furrows associated with all vascular bundles; median bundle (arrowed) indistinguishable structurally from other first order bundles.

D, detail of C with regular, well-developed, flat-topped adaxial ribs and cleft-like furrows.

E, flattened adaxial ribs, steep, deep furrows with well-developed bulliform cell groups at the bases of these furrows.

A, B, *Ellis* 5436; C, D, *Ellis* 2516; E, *Ellis* 2311. A, C, $\times 100$; B, D, E, $\times 250$.

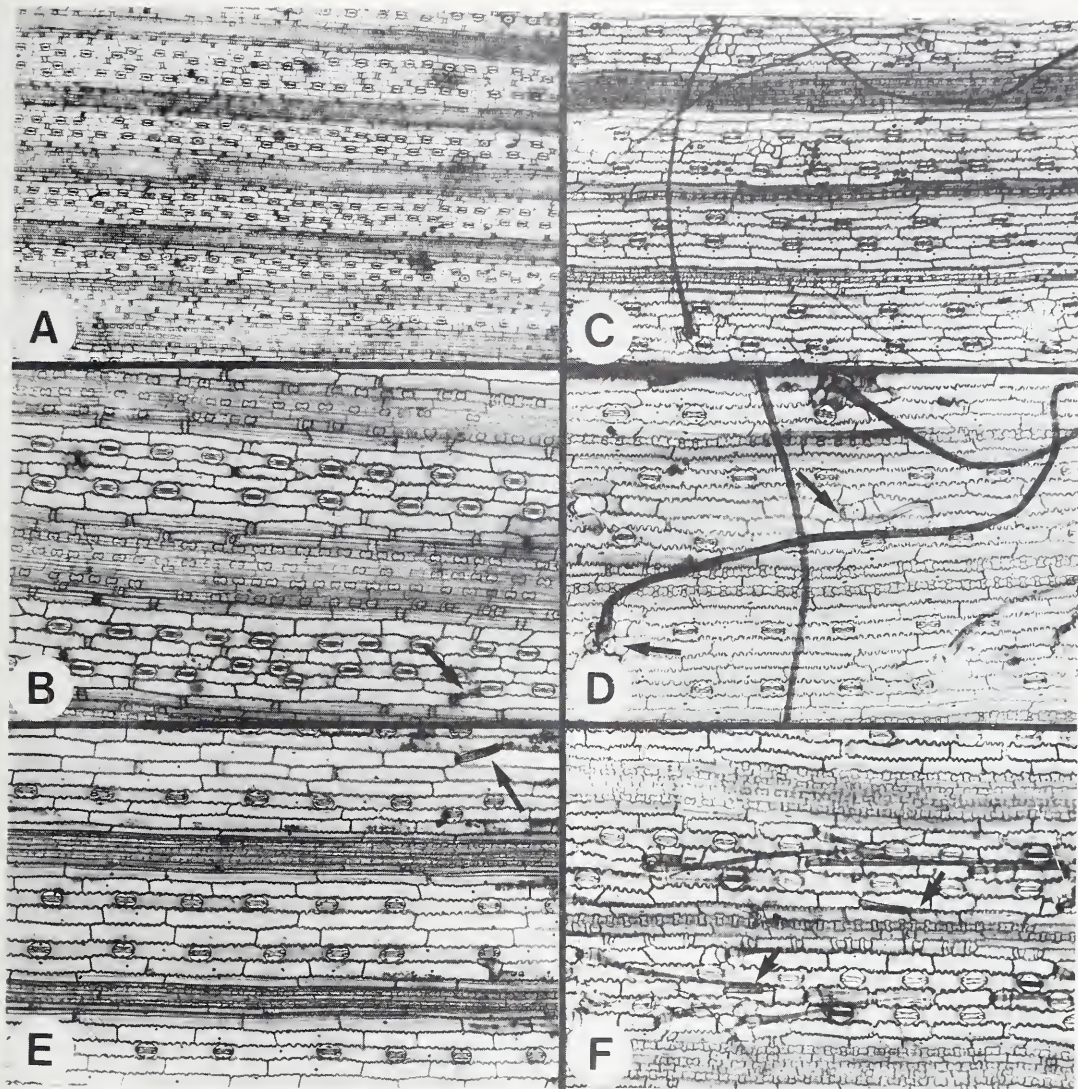


FIGURE 4.2.—*Pentaschistis papillosa*: abaxial epidermis.

A, epidermal zonation with costal and intercostal zones of uniform and regular width.

B, detail showing wide costal zones (7–9 cell files) with small but uniform dumbbell-shaped silica bodies in alternating files; intercostal zones of 6–8 cell files wide with relatively short but rectangular long cells with slightly sinuous cell walls; stomata very common, with dome-shaped subsidiaries; microhairs (arrowed) present.

C, epidermal zonation with long, soft, flexible macrohairs present in intercostal zones; this hair uncommon in this species.

D, detail of macrohair bases in which the hair base is swollen (arrowed) and superficially inserted between a few modified epidermal cells.

E, intercostal zones with rectangular intercostal long cells and stomata; no epidermal appendages except for microhairs (arrowed), these very long with distal cell much shorter than basal cell.

F, shorter macrohairs with swollen bases inserted between specialized, inflated epidermal cells; note very long microhairs (arrowed) which are all more than 3× the length of the stomata.

A, B, *Ellis* 2516; C, D, *Ellis* 5436; E, *Ellis* 5442; F, *Ellis* 5439. A, × 100; C, × 160; B, D–F, × 250.

FIGURE 4.3.—*Pentastichis papillosa*: epidermal ultrastructure. A–D, abaxial epidermis; E–H, adaxial surface.

A, costal zone with shortly-barbed prickles; note macrohairs on intercostal zones.

B, abaxial microhair with basal cell twice as long as distal cell; note relative size of stoma, with microhair at least 3× longer.

C, shorter microhair with very short distal cell.

D, profile of uncommon marginal gland which is neither the stalked, clavate type nor the wrap-around saddle type.

E, adaxial costal rib with small prickles.

F, adaxial microhair with distal cell much shorter than basal cell.

G, adaxial microhairs located on sides of cleft-like furrow; note short, tapering distal cells.

H, unstalked marginal gland showing faint outlines of collar cells; these glands very rare and not conspicuous.

A, B, D–F, *Ellis 5439*; C, G, *Ellis 5436*; H, *Ellis 5442*. A, D, E, × 200; H, × 350; G, × 700; B, F, × 750; C, × 1030.

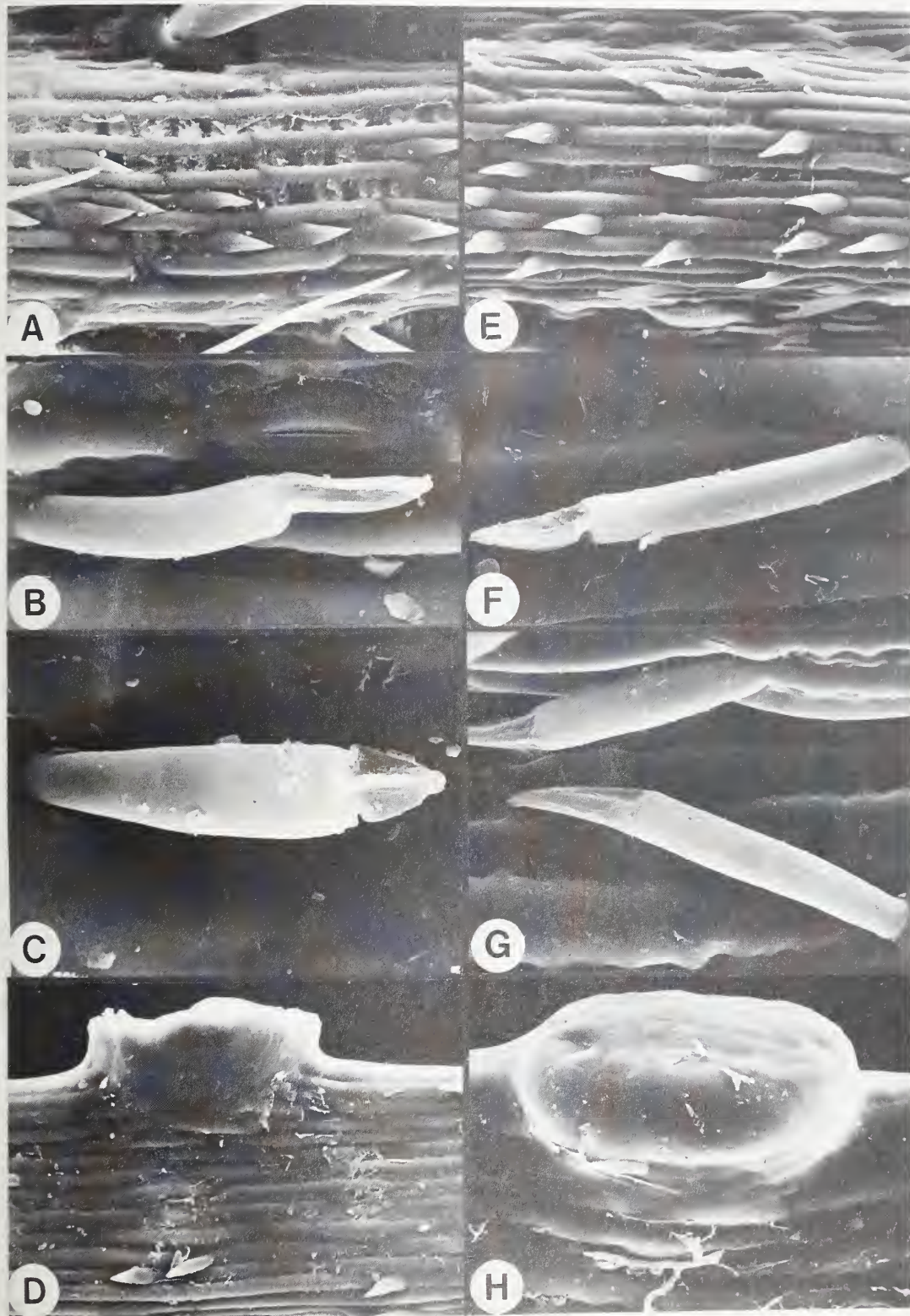


FIGURE 5.1.—*Pentaschistis rupestris*: transectional leaf blade anatomy of specimens with expanded leaf blades.

A, open, expanded blade with margin not tapering; adaxial ribs and furrows very poorly developed.

B, detail of A showing elliptical first order vascular bundles and very diffuse mesophyll with an extensive air space system.

C, slightly inrolled margin of open, expanded leaf blade with margin tapering very slightly; small rounded adaxial ribs and slight furrows present.

D, detail of C illustrating diffuse chlorenchyma of large angular cells exhibiting no pattern of arrangement and large air spaces; note thickness of cuticle on both surfaces.

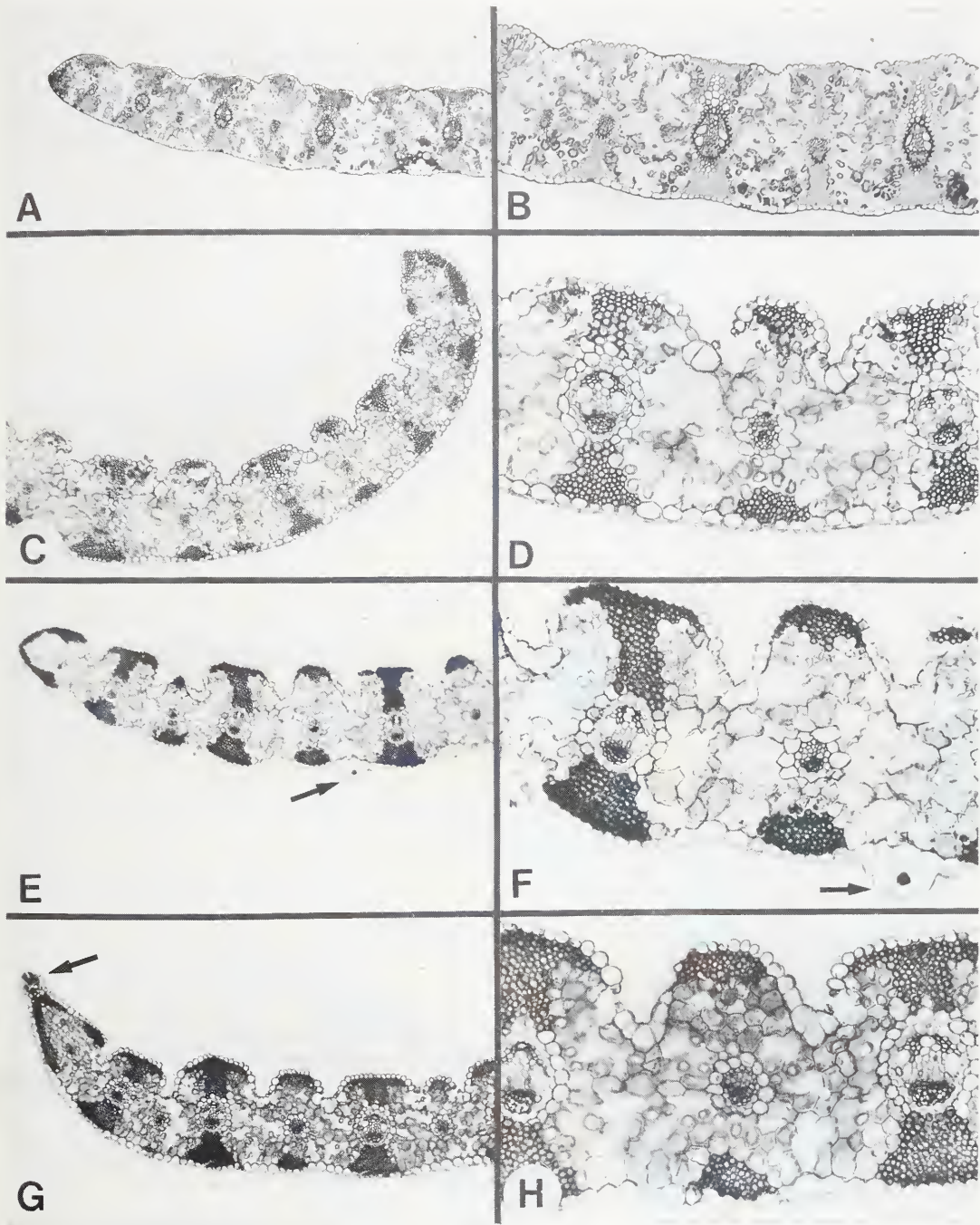
E, expanded, flat outline with medium ribs and furrows; note cushion base of uncommon macrohairs (arrowed), shown in surface view in Figure 5.2B.

F, anatomical detail of E with diffuse, mesic type chlorenchyma, well-developed ribs with T-shaped adaxial girders associated with the first order vascular bundles and strands with the small bundles, and raised cushion base of macrohair (arrowed).

G, tapering margin with rare marginal gland (arrowed) and well-developed adaxial ribs and furrows.

H, anatomical detail of sclerenchyma girders and strands and large angular chlorenchyma cells.

A, B, *Ellis* 2507; C, D, *Ellis* 5504; E, F, *Ellis* 5587; G, H, *Ellis* 5593. A, C, E, G, $\times 100$; B, D, F, H, $\times 250$.



- FIGURE 5.2.**—*Pentaschistis rupestris*: abaxial epidermis of specimens with expanded, open leaf blades.
- A, leaf margin showing marginal clavate glands with short stalks; these glands rare on leaf blades and never very common on a single leaf.
- B, stiff macrohair with small cushion base; this hair type very rare on the leaf blades.
- C, epidermis of very mesic leaf with thin cuticle; note elongated intercostal long cells with slightly undulating anticlinal walls, stomata widely spaced due to single, elongated interstomatal long cell and microhairs common.
- D, epidermis of leaf with thicker cuticle than that of C; note long cells shorter with thicker, more sinuous walls and stomata closer together but cell pattern identical.
- E, sinuous-walled long cells, dome-shaped stomatal subsidiaries, and basal cells of microhairs (arrowed) from leaf with thick cuticle.
- F, epidermal detail with stomatal files and long cells with sinuous walls.
- G, costal zone with few prickles with short barbs and detail of microhair (arrowed) with distal cell longer than basal cell.
- H, note thick, sinuous anticlinal walls of rectangular long cells without stomatal files; very unusual microhair (arrowed) which consists of three cells.
- A, B, *Ellis* 5587; C, *Ellis* 2505; D, *Ellis* 5506; E, *Ellis* 5593; F, *Ellis* 5504; G, *Ellis* 5788; H, *Ellis* 5792. A, \times 100; B–D, \times 160; E–H, \times 250.

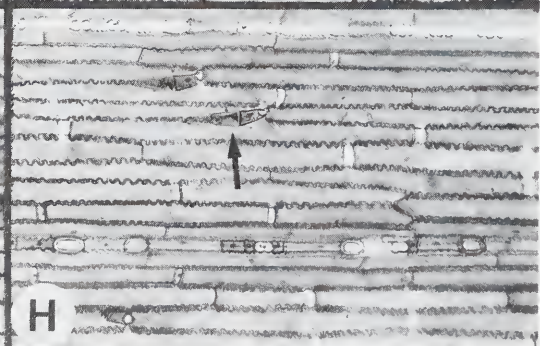
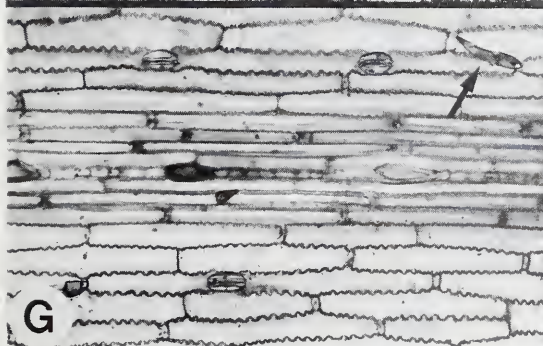
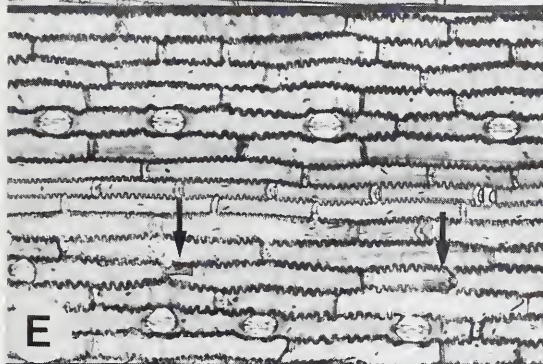
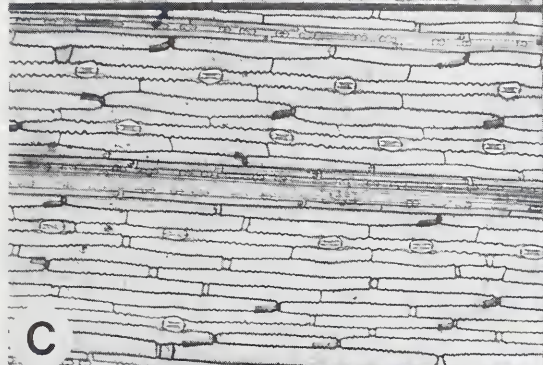
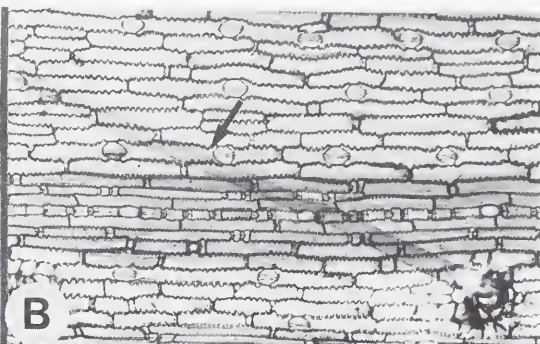
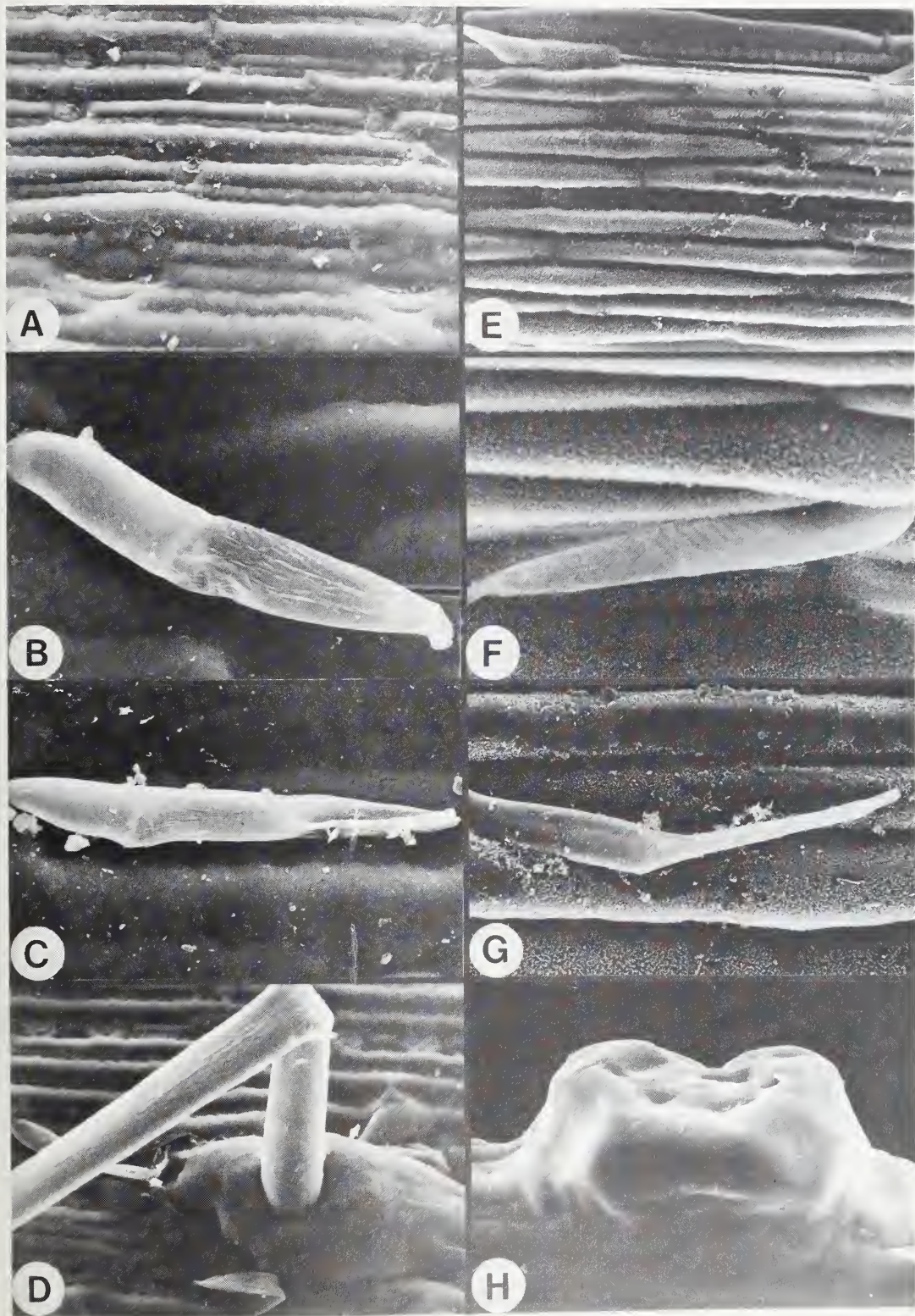


FIGURE 5.3.—*Pentascistis rupestris*: SEM of specimens with expanded leaves. A–D, abaxial epidermis; E–H, adaxial epidermis.

- A, very thick and sinuous anticlinal walls and inflated periclinal walls of intercostal long cells; note two stomata located at a lower level than the inflated periclinal long cells.
B, finger-like microhair with basal cell slightly longer than the tapering distal cell.
C, tricellular microhair showing the typical shorter basal cell and two longer distal cells.
D, detail of raised cushion of macrohair.
E, adaxial long cells with inflated periclinal walls but anticlinal walls not thickened and sinuous.
F, adaxial microhair with basal and distal cells of equal length.
G, finger-like microhair with collapsed distal cell; basal and distal cells equal in length.
H, marginal gland with very short stalk.
A, E, H, *Ellis* 5593; B, D, F, *Ellis* 5587; C, G, *Ellis* 5792. A, D, E, $\times 210$; H, $\times 300$; C, G, $\times 460$; B, F, $\times 630$.



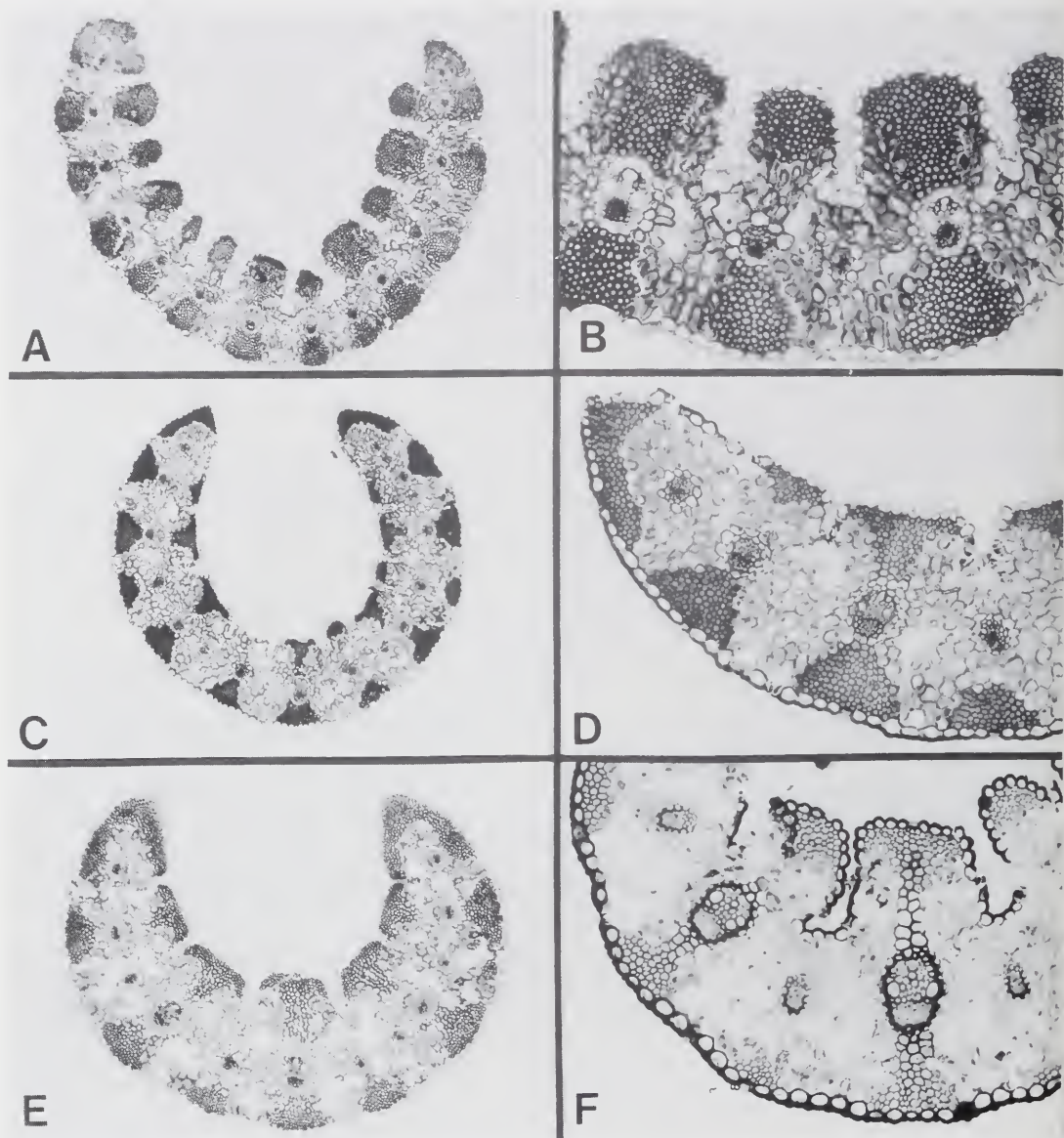


FIGURE 5.4.—*Pentaschistis rupestris*: transectional leaf anatomy of specimens with narrow, inrolled leaves. A, narrow, inrolled leaf outline with well-developed adaxial ribs and furrows and even slight abaxial ribbing associated with the vascular bundles. B, detail of A showing large adaxial and abaxial sclerenchyma girders associated with all the vascular bundles; note diffuse nature of the chlorenchyma tissue. C, inrolled, almost canaliculate outline. D, detail of well-developed girders and mesic type mesophyll. E, narrow, inrolled setaceous leaf. F, anatomical detail of adaxial ribs and furrows, sclerenchyma fibres and diffuse mesophyll with extensive air spaces. A, B, *Ellis 5577*; C, D, *Ellis 5484*; E, *Ellis 5597*; F, *Ellis 5598*. A, C, E, $\times 100$; B, D, F, $\times 250$.

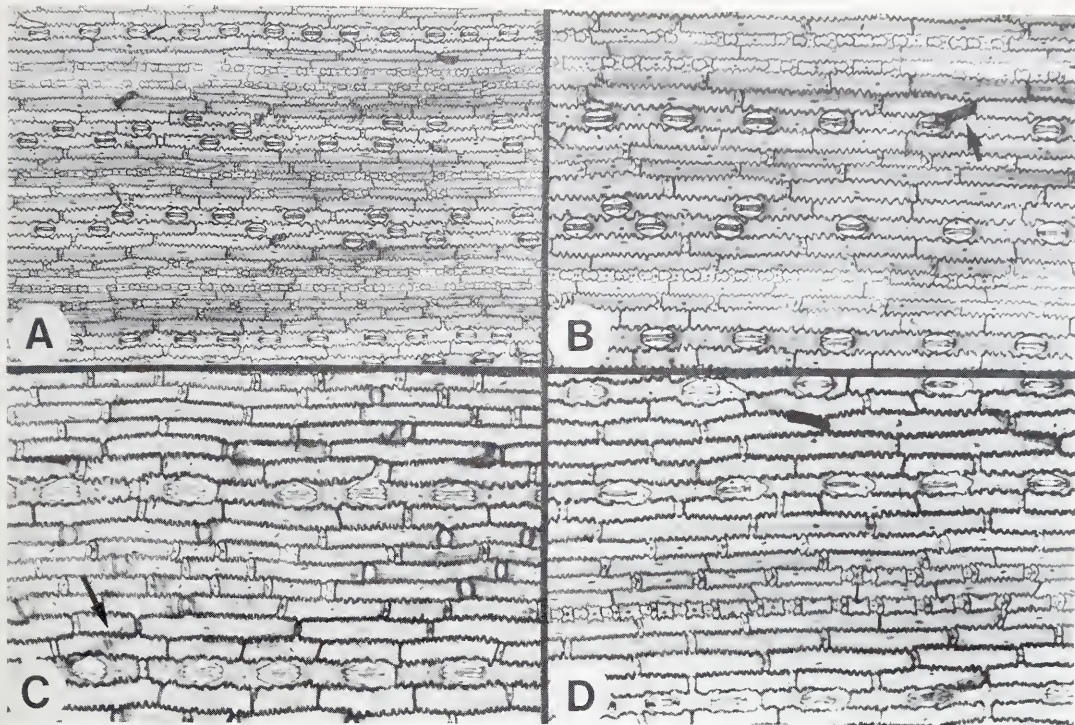


FIGURE 5.5.—*Pentaschistis rupestris*: abaxial epidermis of specimens with inrolled, strengthened leaf blades. A, epidermal zonation with relatively wide costal zones (5–7 files wide) and narrower intercostal zones (3–5 files wide). B, detail of A with irregularly dumbbell-shaped silica bodies, low dome-shaped subsidiary cells and single microhair (arrowed). C, epidermal detail with shortly rectangular intercostal long cells with thickened, sinuous walls, stomata and microhairs (arrowed). D, relative length of microhairs noteworthy, being more than 3× the length of the stomata; many stomata with unusual short cell enfolding subsidiary cells.

A, B, *Ellis 5484*; C, *Ellis 5598*; D, *Ellis 5597*. A, × 160; B–D, × 250.

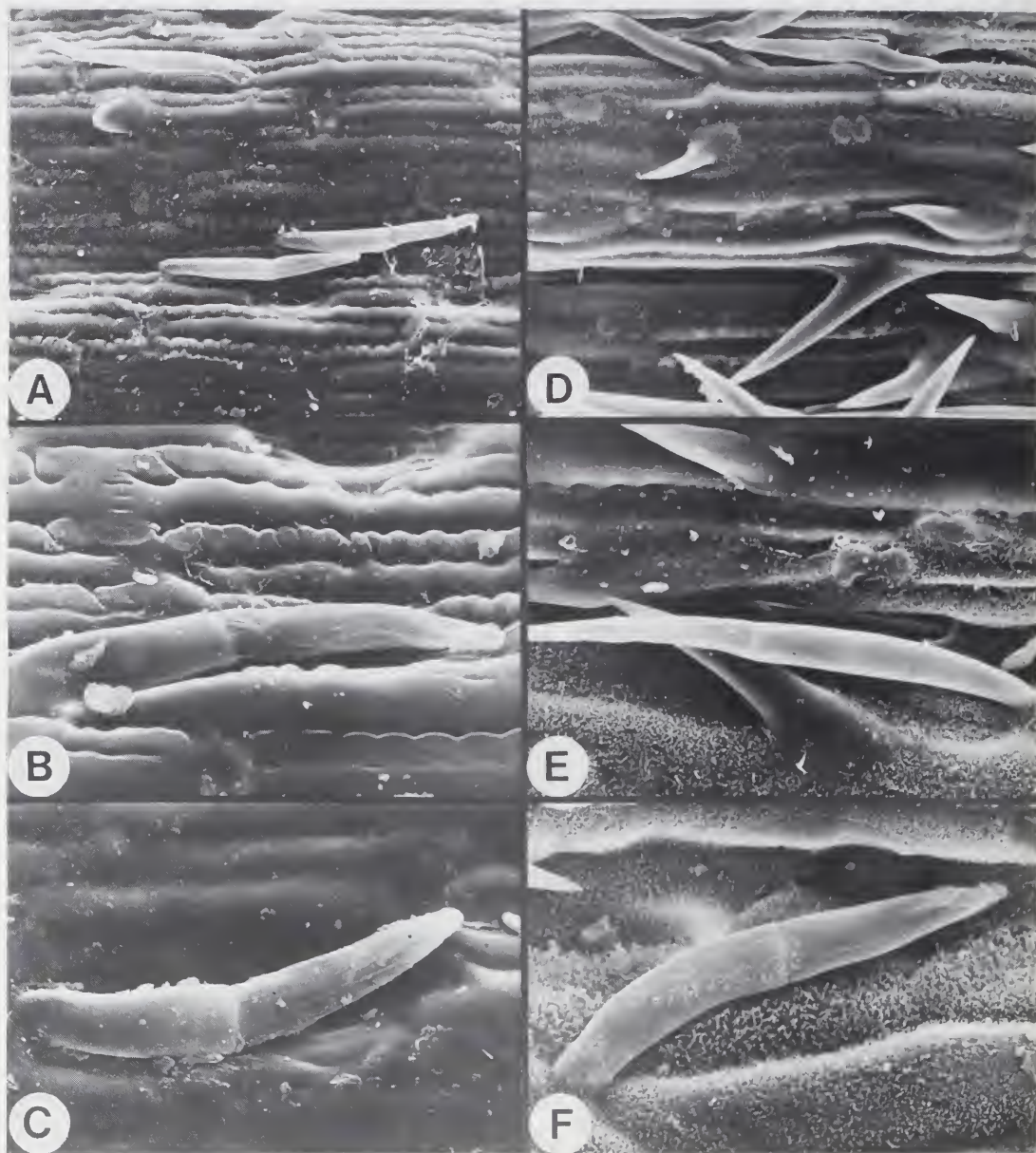


FIGURE 5.6.—*Pentaschistis rupestris*: epidermal ultrastructure of specimens with thickened, rolled leaves. A–C, abaxial epidermis; D–F, adaxial epidermis.

A, anticlinal long cell walls thickened and sinuous; note large relative size of the finger-like microhairs.

B, elongate microhair with distal cell slightly longer than basal cell.

C, abaxial bicellular microhair with tapering distal cell which is slightly longer than the basal cell.

D, adaxial rib showing prickly hairs with long barbs, microhairs and silica bodies.

E, unusual very thin elongated microhair but relative lengths of basal and distal cell remain about equal.

F, more normal thicker adaxial microhair comprised of two equally long cells.

A, B, D, E, *Ellis 5577*; C, F, *Ellis 5597*. A, D, $\times 200$; C, E, $\times 450$; B, F, $\times 570$.

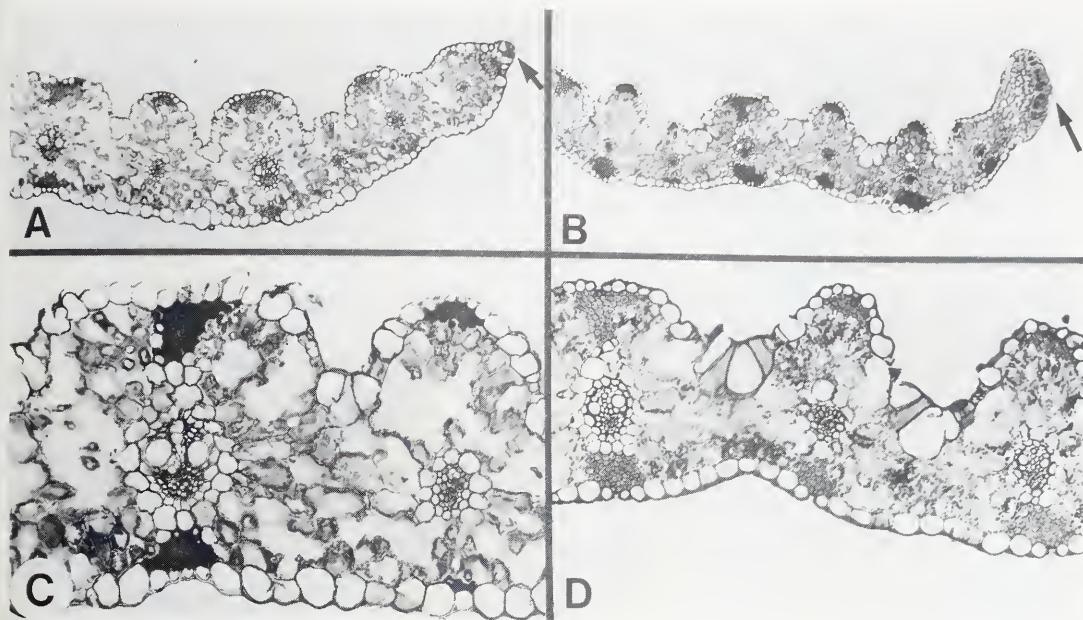


FIGURE 6.1.—*Pentaschistis longipes*: transectional leaf blade anatomy.

A, expanded, thick leaf with adaxial ribs and furrows and with marginal gland (arrowed).

B, margin showing abaxial marginal gland without stalk (arrowed).

C, detail of diffuse chlorenchyma with extensive air spaces, small sclerenchyma girders associated with the first order bundles and strands with the small bundles, and thin cuticle.

D, well-developed bulliform cells at the bases of the adaxial furrows.

A, C, *Ellis 6006*; B, D, *Linder 5048*. A, B, $\times 100$; C, D, $\times 250$.

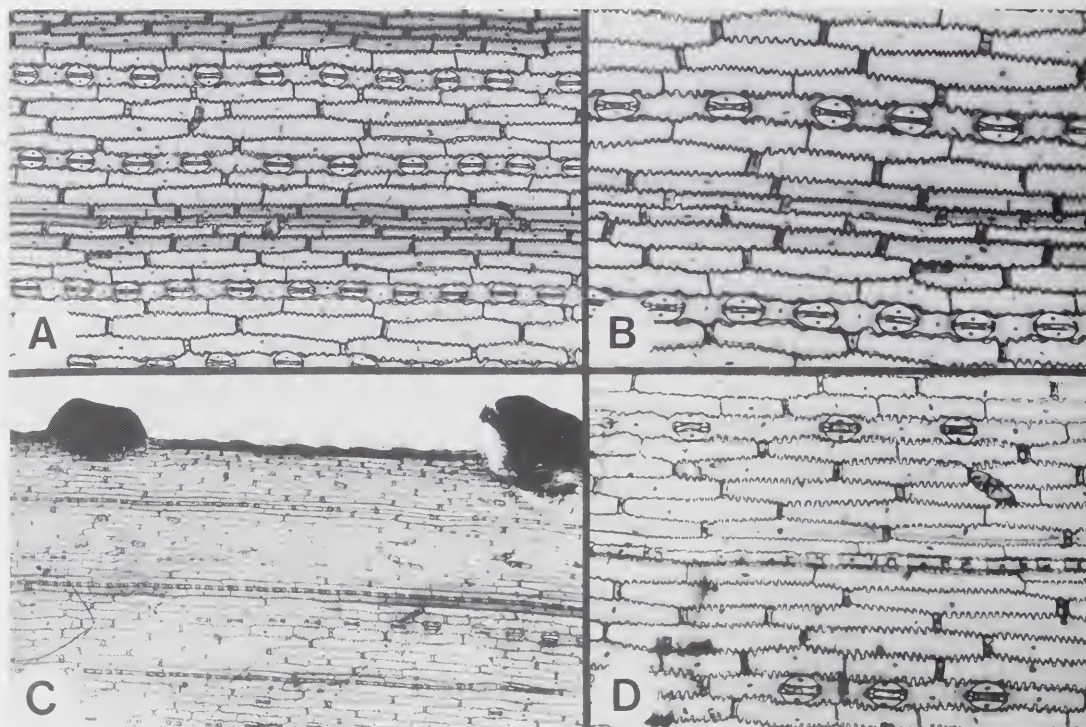


FIGURE 6.2.—*Pentaschistis longipes*: abaxial epidermis.

A, zonation showing relatively undifferentiated costal zones and wide intercostal zones with files of stomata.

B, detail of low dome-shaped stomata separated by short interstomatal cells, sinuous long cells and large microhairs.

C, slightly raised marginal glands.

D, cellular detail similar to B; note very wide microhairs.

A, B, *Ellis 6006*; C, D, *Linder 5048*. C, $\times 100$. A, $\times 160$; B, D, $\times 250$.

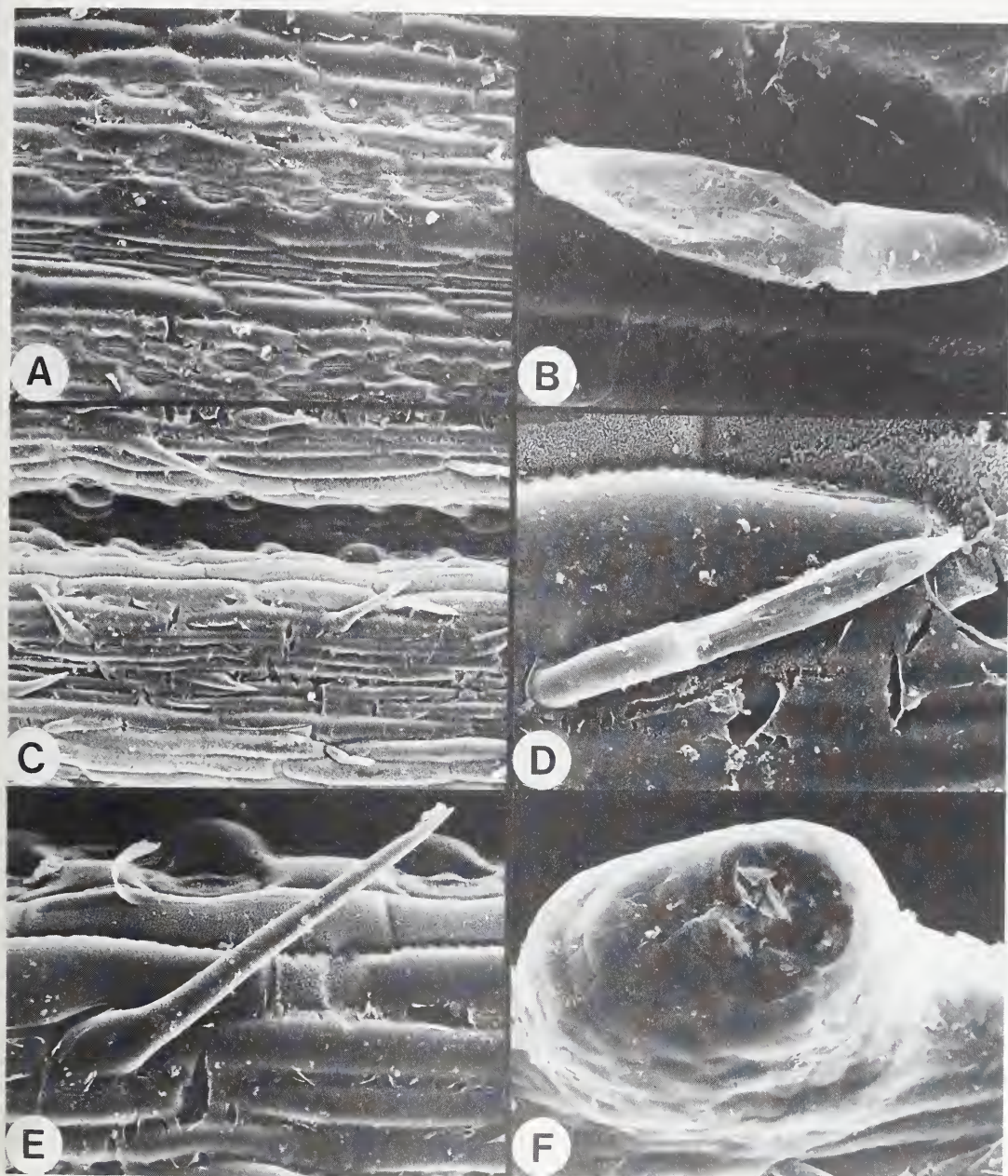


FIGURE 6.3.—*Pentaschistis longipes*: leaf blade surface ultrastructure. A, B, abaxial surface; C–F, adaxial surface.

A, relatively featureless abaxial epidermis but note close spacing of stomata along files.

B, microhair with distal cell twice as long as basal cell.

C, small prickles on adaxial ribs; note microhairs on ribs as well.

D, narrow, finger-like adaxial microhair, much longer than abaxial hairs (compare magnifications).

E, detail of prickly barb.

F, slightly raised marginal gland.

A–F, *Ellis 6006*. A, C, $\times 60$; E, $\times 170$; F, $\times 200$; D, $\times 350$; B, $\times 580$.

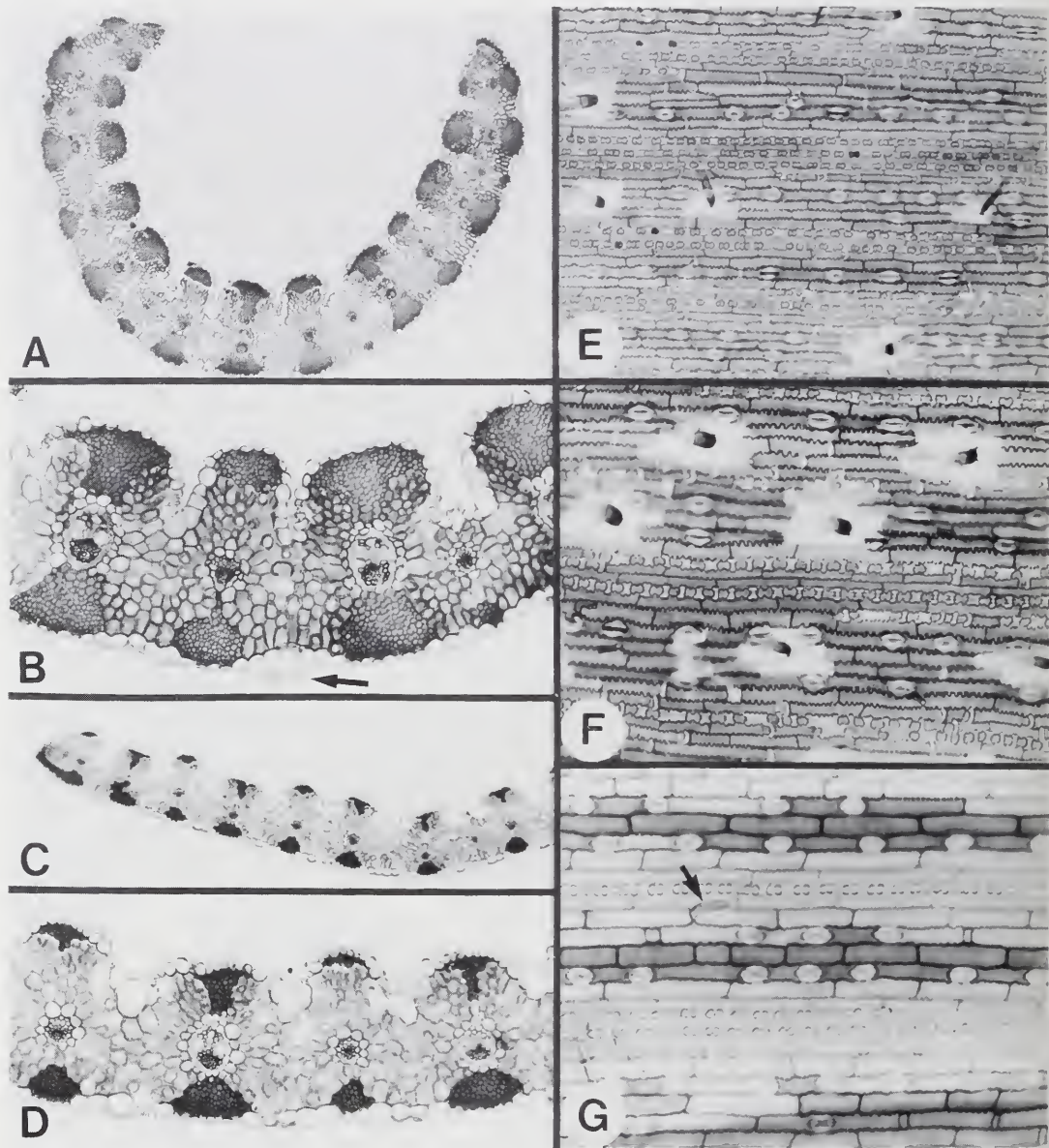


FIGURE 7a.1.—*Pentaschistis pallida* form A 'brevifolia': leaf anatomy in transection and epidermal surface view.

A–D, blade in transverse section. E–G, abaxial epidermis.

A, outline of lamina showing narrow, inrolled blade with abrupt margin.

B, detail of sclerenchyma girders, ribs and furrows and somewhat compact mesophyll; note base of macrohair (arrowed).

C, outline of open, expanded blade.

D, cellular detail of sclerenchyma tissue with non-lignified secondary walls.

E, epidermal zonation with relatively narrow intercostal zones with only 1–2 stomatal files.

F, detail of irregularly dumbbell-shaped silica bodies and short intercostal long cells with sinuous walls; note macrohairs with few unstained, specialized epidermal cells associated with their bases.

G, intercostal and costal long cells differentially stained; note microhair (arrowed).

A, B, E, F, *Ellis* 704; C, D, G, *Ellis* 647. A, C, $\times 100$; E, $\times 160$; B, D, E, G, $\times 250$.



FIGURE 7b.1.—*Pentaschistis pallida* form B ‘pallida’: leaf transverse sections of specimens resembling form A in leaf anatomy.

A, leaf outline showing narrow leaf blade.

B, detail of abrupt margin, adaxial ribs and furrows and well-developed girders and strands.

C, inrolled, narrow, leaf blade.

D, anatomical detail showing characteristic xerophytic features of form A.

E, ribs, girders and margin typical of this form.

F, well-developed girders, with fibres with cellulose secondary walls, showing lateral girders fused abaxially.

A, B, *Ellis* 2210; C, D, *Ellis* 2262; E, *Ellis* 2215; F, *Ellis* 5827. A, C, $\times 100$; B, D–F, $\times 250$.

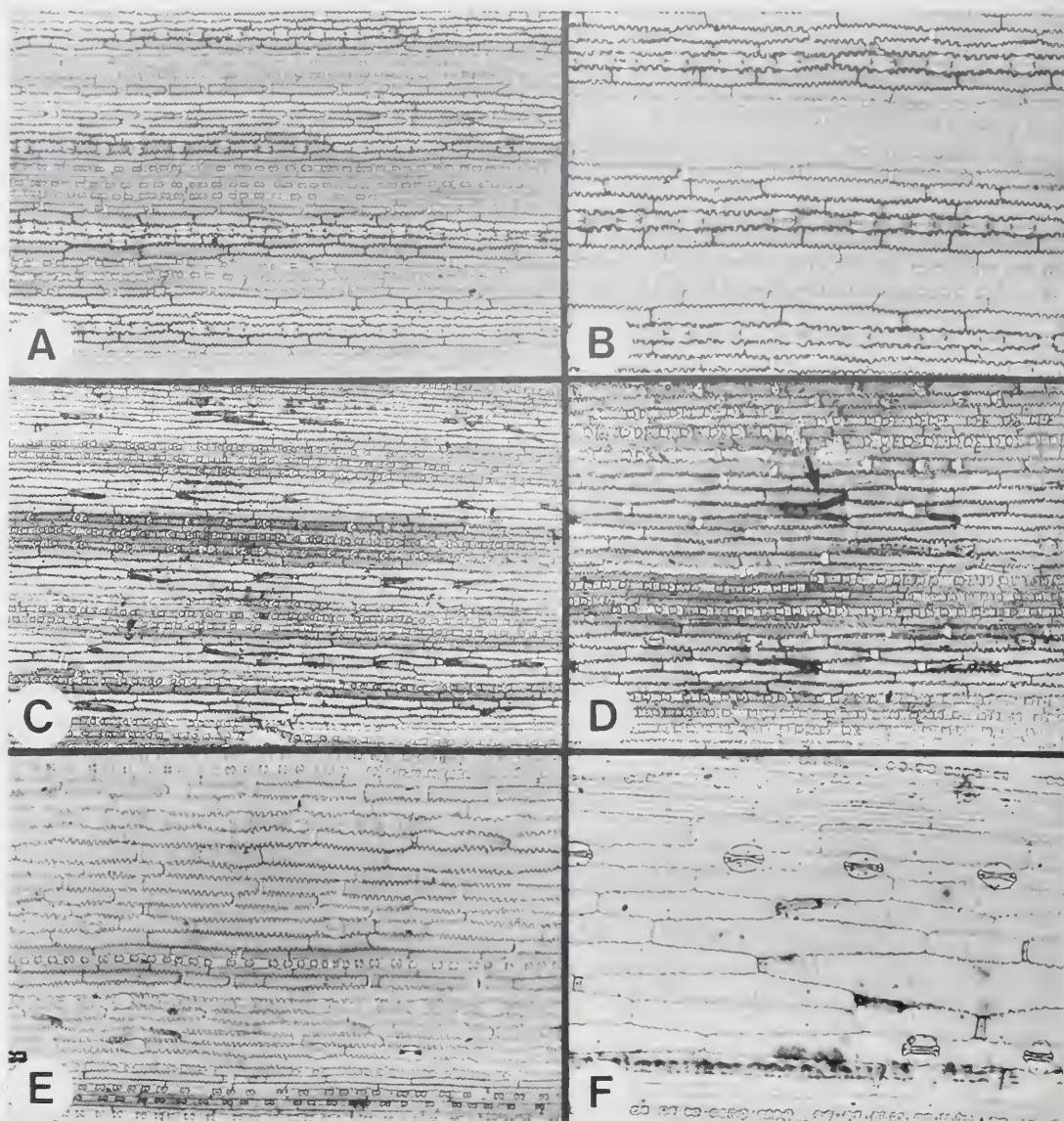


FIGURE 7b.2.—*Pentaschistis pallida* form B 'pallida': abaxial epidermis of specimens resembling form A in leaf anatomy.

A, epidermal zonation with costal and intercostal zones of similar width.

B, detail of A showing irregular dumbbell-shaped silica bodies, sinuous intercostal long cells and single file of stomata per intercostal zone.

C, typical epidermal pattern of this type.

D, costal and intercostal zone detail; note conspicuous and numerous microhairs (arrowed).

E, xerophytic type epidermis with few stomata and short intercostal long cells with sinuous anticlinal walls.

F, example of more mesic type epidermal structure with longer, less sinuous intercostal long cells, stomata and microhairs; this epidermis similar to that of typical form B specimens except that no glands or macrohairs are present.

A, B, *Ellis* 1176; C, D, *Ellis* 5827; E, *Ellis* 2262; F, *Ellis* 2210. A, C, $\times 160$; B, D, E, $\times 250$; F, $\times 400$.

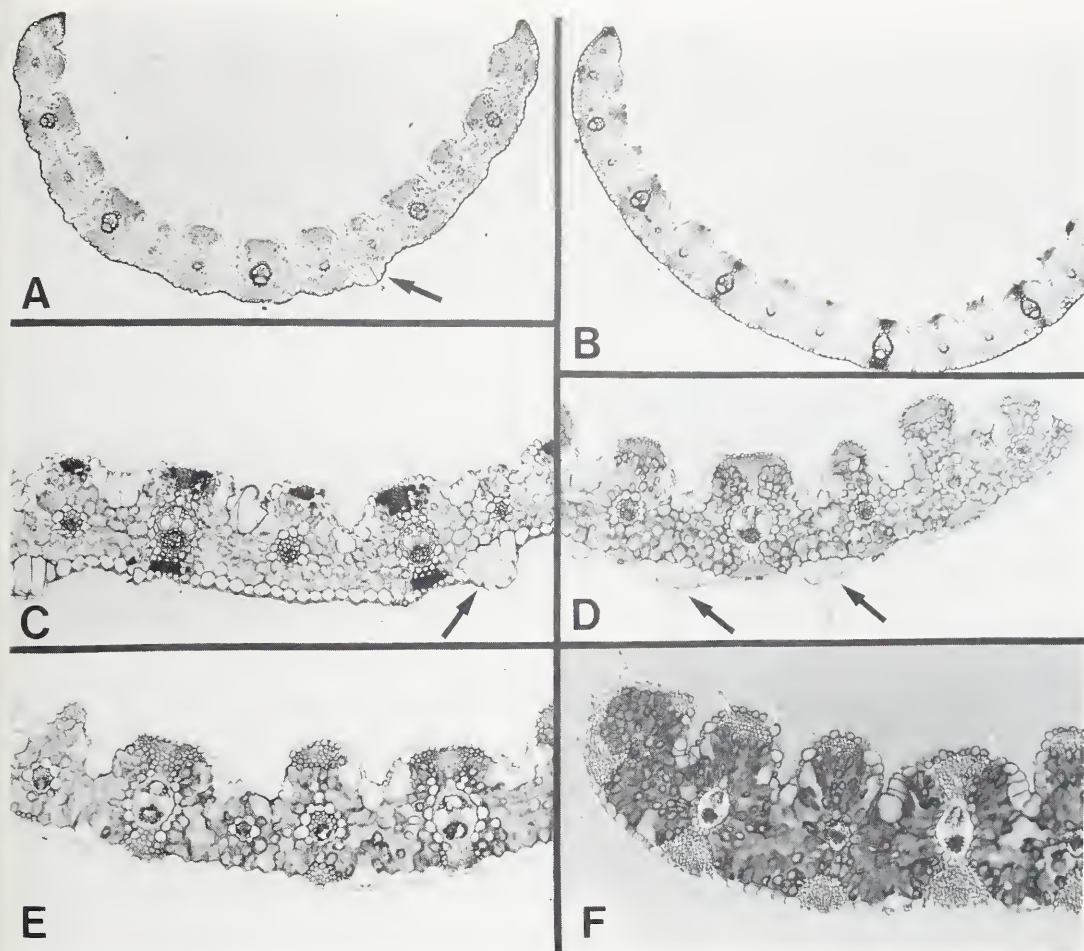


FIGURE 7b.3. — *Pentaschistis pallida* form B '*pallida*': transverse sections of typical form B specimens with macrohairs but glands not seen or not visible on leaf segment examined.

A, outline showing thinner and wider leaf blade than in the form A type; macrohair base arrowed.

B, wide, thin leaf.

C, anatomical detail of small ribs, shallow, wide furrows and small sclerenchyma girders and strands, often not developed abaxially in association with the third order bundles; note raised cushion bases of macrohairs (arrowed).

D, slightly tapering margin and macrohair bases (arrowed).

E, typical mesic type anatomy.

F, specimen with abrupt margin and thicker leaf, resembling form A but macrohairs common (see Figure 7b.5G).

A, *Ellis 1191*; B, E, *Ellis 2223*; C, *Ellis 5127*; D, *Ellis 2312*; F, *Ellis 2316*. A, B, $\times 100$; C–F, $\times 250$.

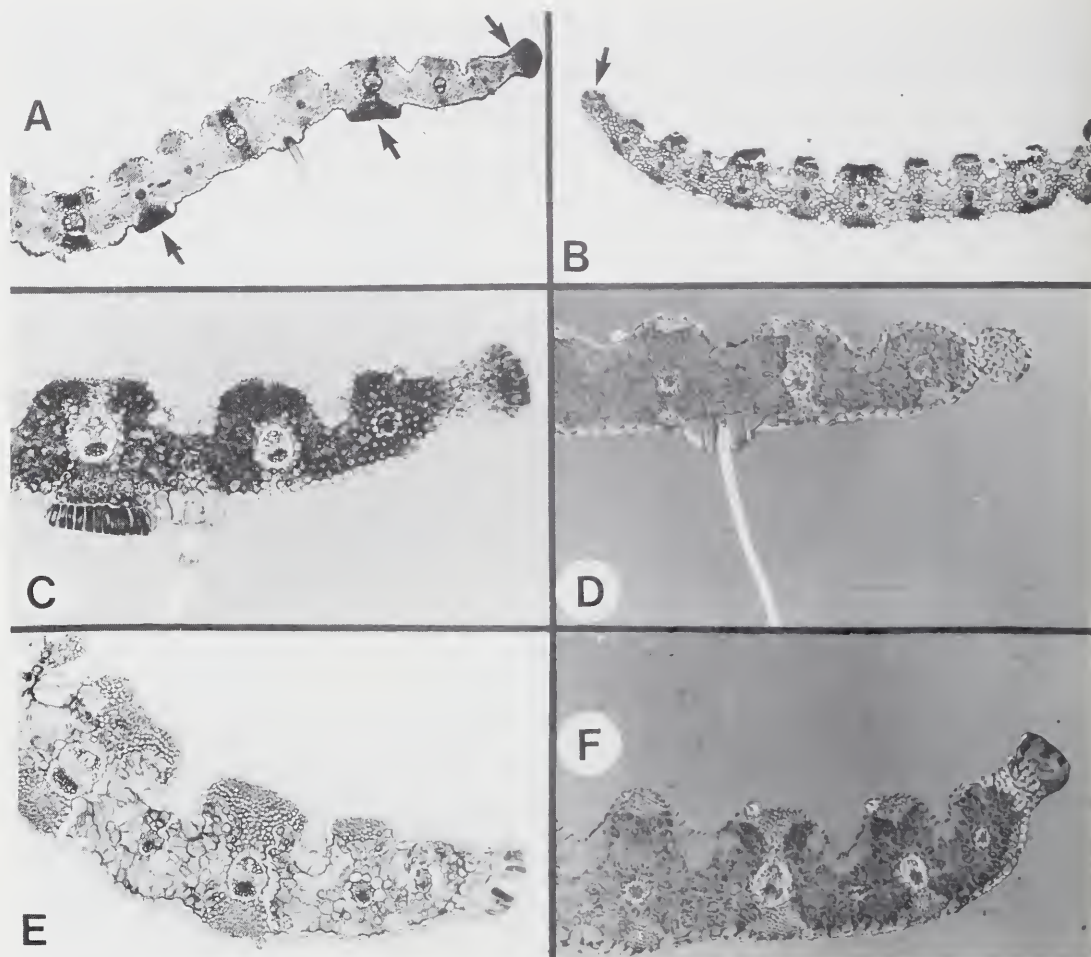
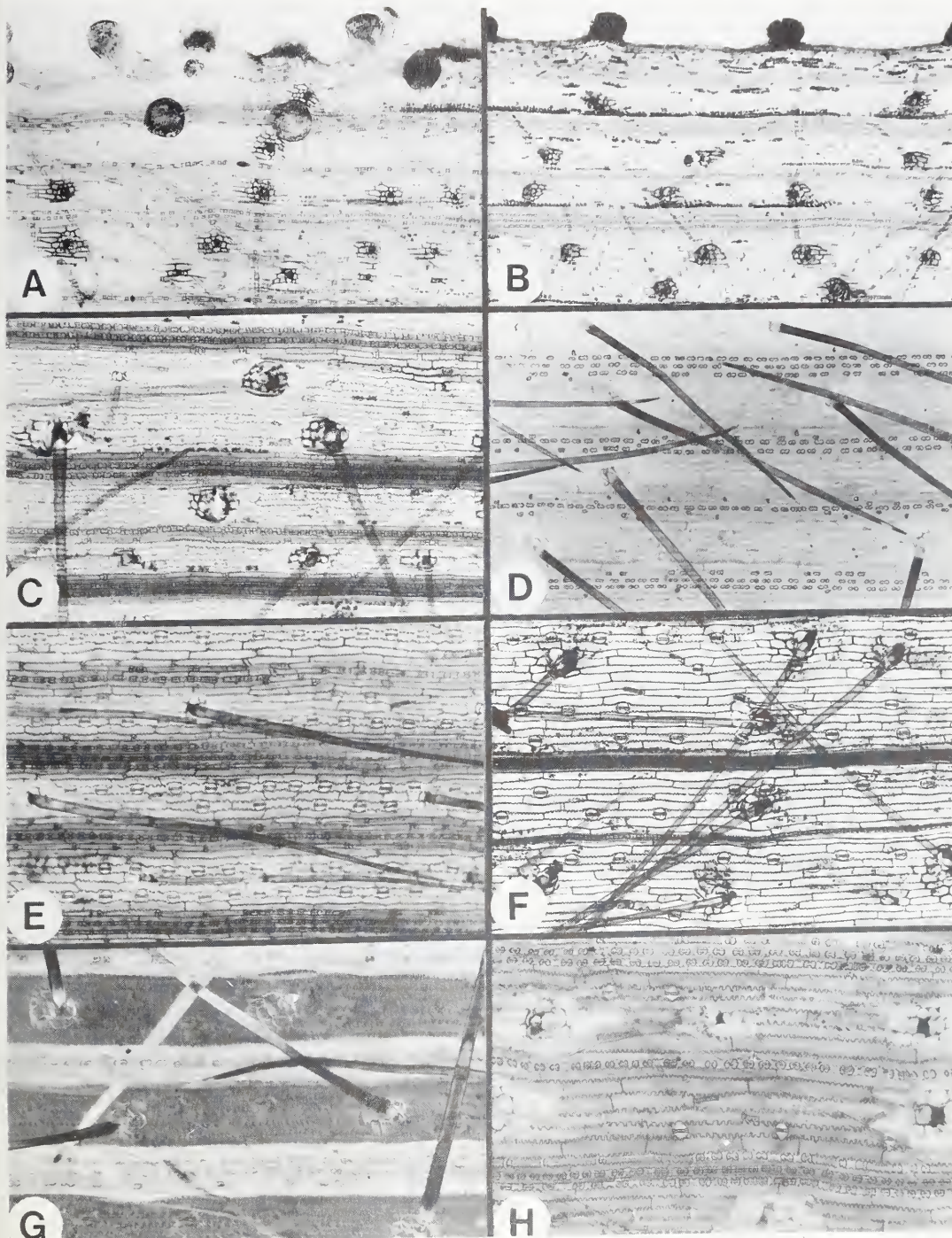


FIGURE 7b.4.—*Pentaschistis pallida* form B 'pallida': transverse sections of typical form B specimens with stalked glands and/or macrohairs.

- A, very glandular specimen with marginal and abaxial glands (arrowed) resembling those of *P. aspera*; note expanded, thin leaf outline and macrohair bases.
 B, thin, expanded but relatively wide leaf blade with marginal glands (arrowed).
 C, detail of marginal and abaxial glands and macrohair base.
 D, interference contrast of lateral gland and cushion-based macrohair.
 E, margin with gland; note xerophytic or cryophytic features associated with high altitude—ribs and narrow furrows, well-developed sclerenchyma girders and narrow, inrolled blade.
 F, interference contrast of stalked marginal gland. A, C, *Ellis* 2489; B, *Ellis* 5470; D, *Ellis* 1162; E, *Ellis* 5508; F, *Ellis* 1192. A, B, $\times 100$; C–F, $\times 250$.

FIGURE 7b.5.—*Pentaschistis pallida* form B 'pallida': abaxial epidermis of typical specimens with stalked glands and macrohairs.

- A, lateral part of blade showing numerous marginal glands as well as abaxial glands and macrohairs; this closely resembles the epidermis of *P. aspera*.
 B, raised marginal glands and numerous macrohairs with raised cushion bases.
 C, macrohairs with raised cushion bases; note relatively wide costal zones of high altitude specimen with xerophytic features.
 D, dense indumentum of stiff macrohairs arising from the intercostal zones.
 E, long, stiffened macrohairs with base constrictions visible.
 F, very long macrohairs on a typically mesic leaf with narrow costal zones and wide intercostal zones with elongated long cells.
 G, detail of high altitude specimen with wider costal zones; note thick-walled macrohairs with raised cushion bases.
 H, epidermal detail showing differentially staining cushion cells associated with the macrohair bases.
 A, *Ellis* 2489; B, *Ellis* 1191; C, *Ellis* 5508; D, G, *Ellis* 2316; E, *Ellis* 5470; F, *Ellis* 5127; H, *Ellis* 1162. A–F, $\times 160$; G, H, $\times 250$.



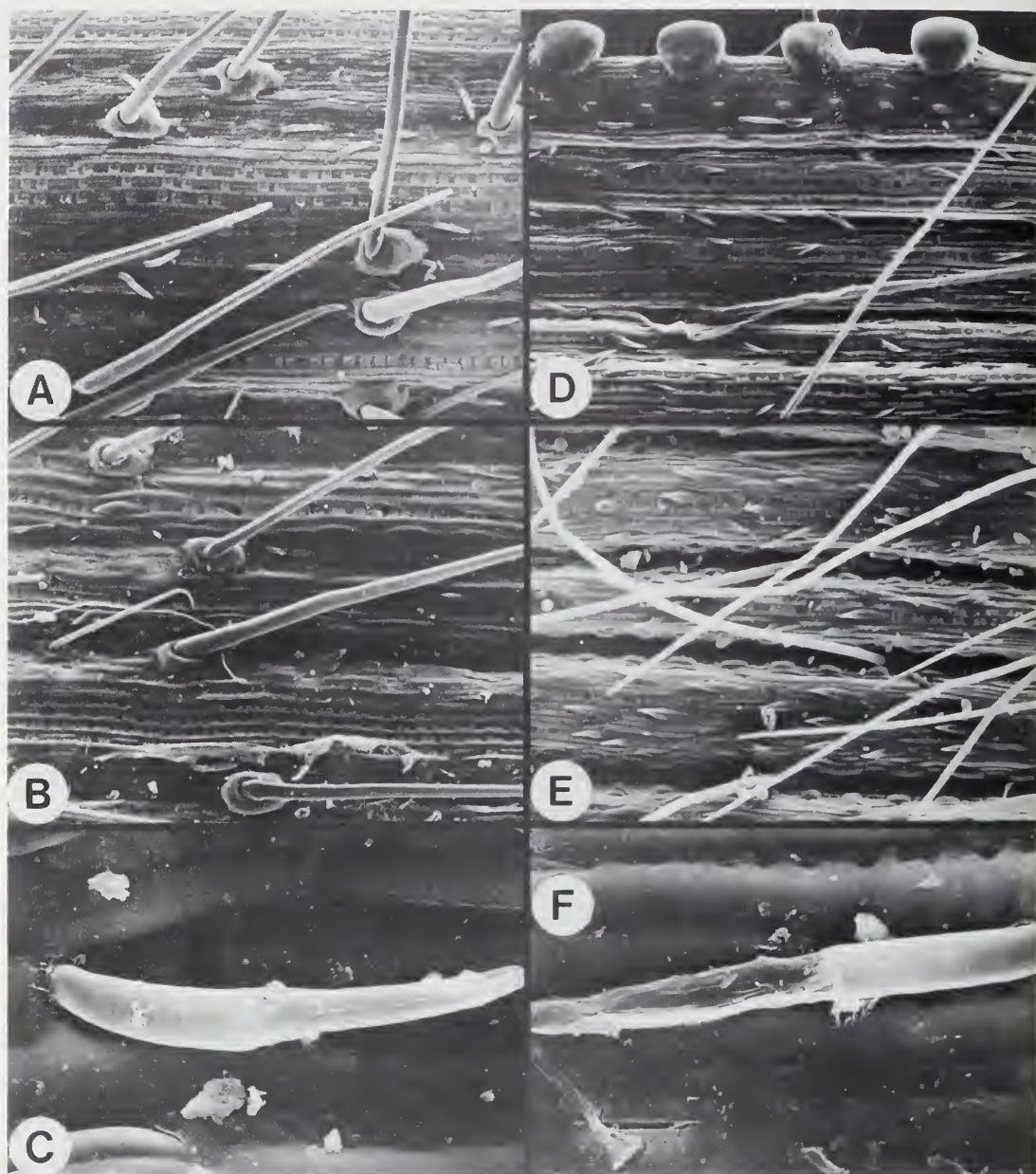


FIGURE 7b.6.—*Pentaschistis pallida* form B 'pallida': leaf blade ultrastructure. A–C, abaxial epidermis. D–F, adaxial epidermis.

A, stiff macrohairs with raised bases in intercostal zones.

B, stiff macrohairs with raised cushion bases.

C, elongated microhair with tapering distal cell of same length as the basal cell.

D, margin with raised glands and adaxial macrohairs thin and elongated.

E, flexible, thin adaxial macrohairs arising from intercostal furrows.

F, finger-like macrohair with both cells of similar length; note stomatal pore.

A, E, *Ellis* 5508; B, E, F, *Ellis* 5470; C, *Ellis* 5127. A, B, D, E, $\times 60$; C, F, $\times 650$.

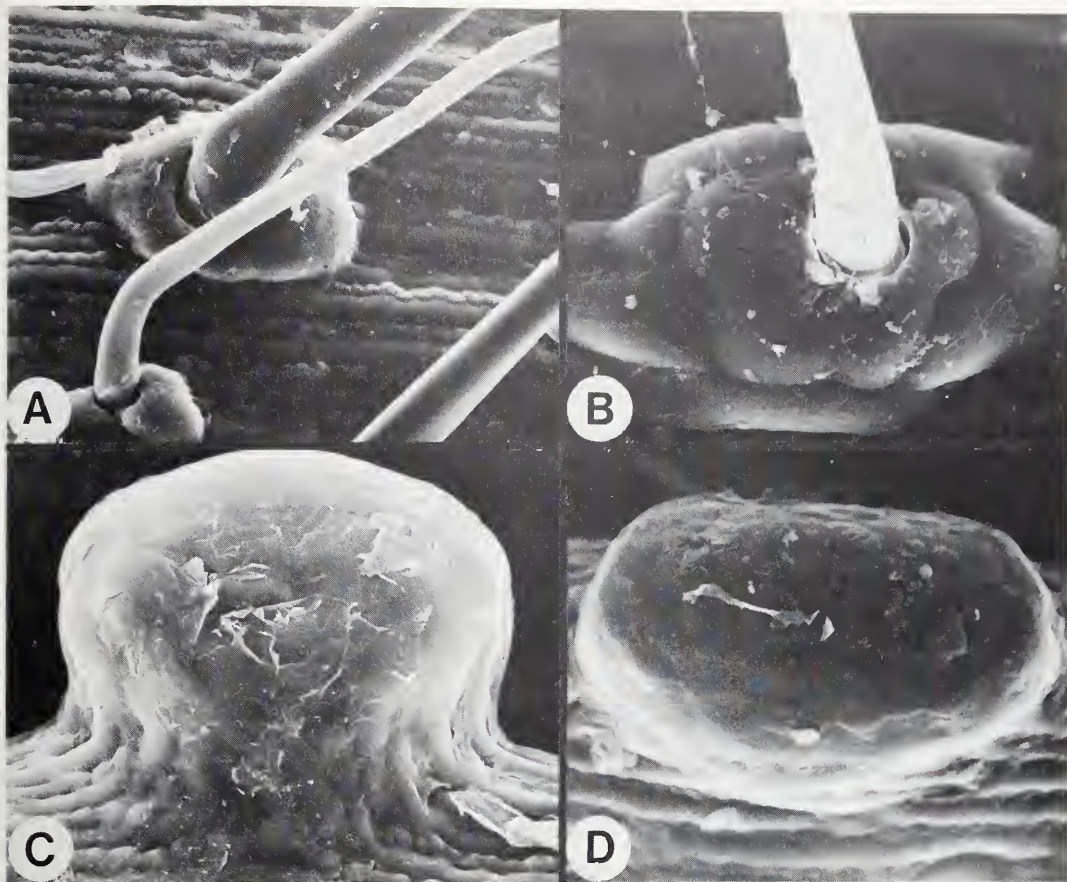


FIGURE 7b.7.—*Pentaschistis pallida* form B 'pallida': ultrastructural detail of macrohairs and glands. A, B, abaxial macrohairs. C, D, marginal glands.

A, raised cushion bases of macrohairs.

B, detail of hair insertion between raised cushion cells.

C, profile of short-stalked marginal gland.

D, short-stalked marginal gland which is not typically club-shaped.

A, C, *Ellis 5508*; B, *Ellis 5127*; D, *Ellis 5470*. A, $\times 250$; B–D, $\times 400$.

FIGURE 7b.8. — *Pentaschistis pallida* form B 'pallida': anatomy of an example of the specialized high altitude plants which are included in this taxon. A, B, leaf in transection. C, D, abaxial epidermis. E–H, epidermal ultrastructure.

A, very narrow needle-like acicular outline; marginal glands arrowed.

B, detail of diffuse chlorenchyma tissue, abaxial hypodermal sclerenchyma layer and marginal gland (arrowed).

C, leaf margin showing numerous raised glands.

D, abaxial epidermis illustrating virtual absence of zonation and stomata; silica bodies unusual in not being dumbbell-shaped.

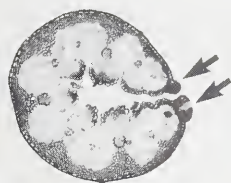
E, abaxial epidermis with microhairs but no other epidermal appendages.

F, microhair detail showing relatively thick hair but with cells of equal length.

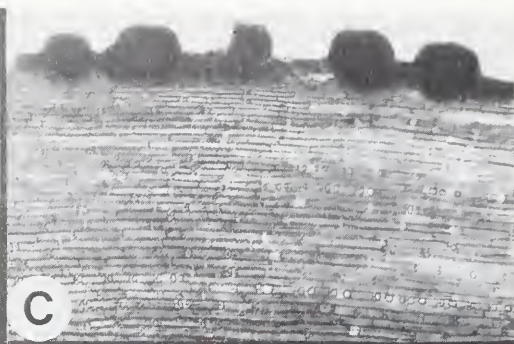
G, adaxial epidermis with short hooks and stomata confined to cleft-like furrows.

H, marginal gland.

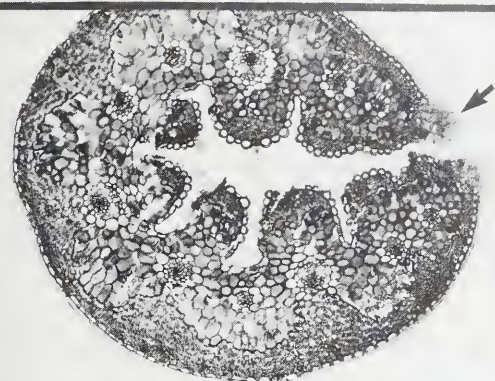
A–H, *Linder* 4429. A, $\times 100$; C, $\times 160$; E, G, $\times 200$; B, D, $\times 250$; H, $\times 380$; F, $\times 850$.



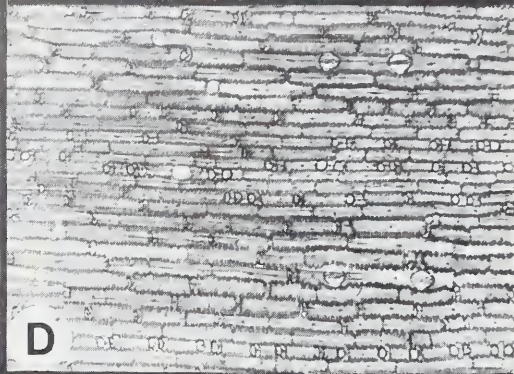
A



C



B



D



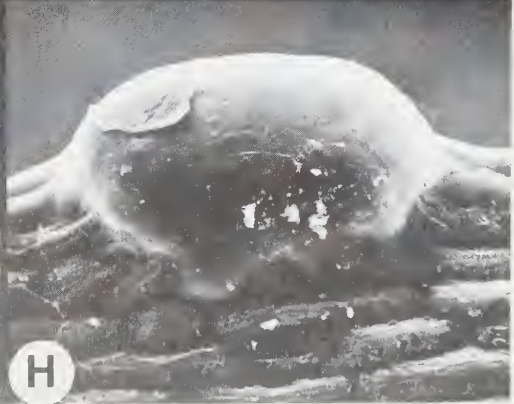
E



G



F



H

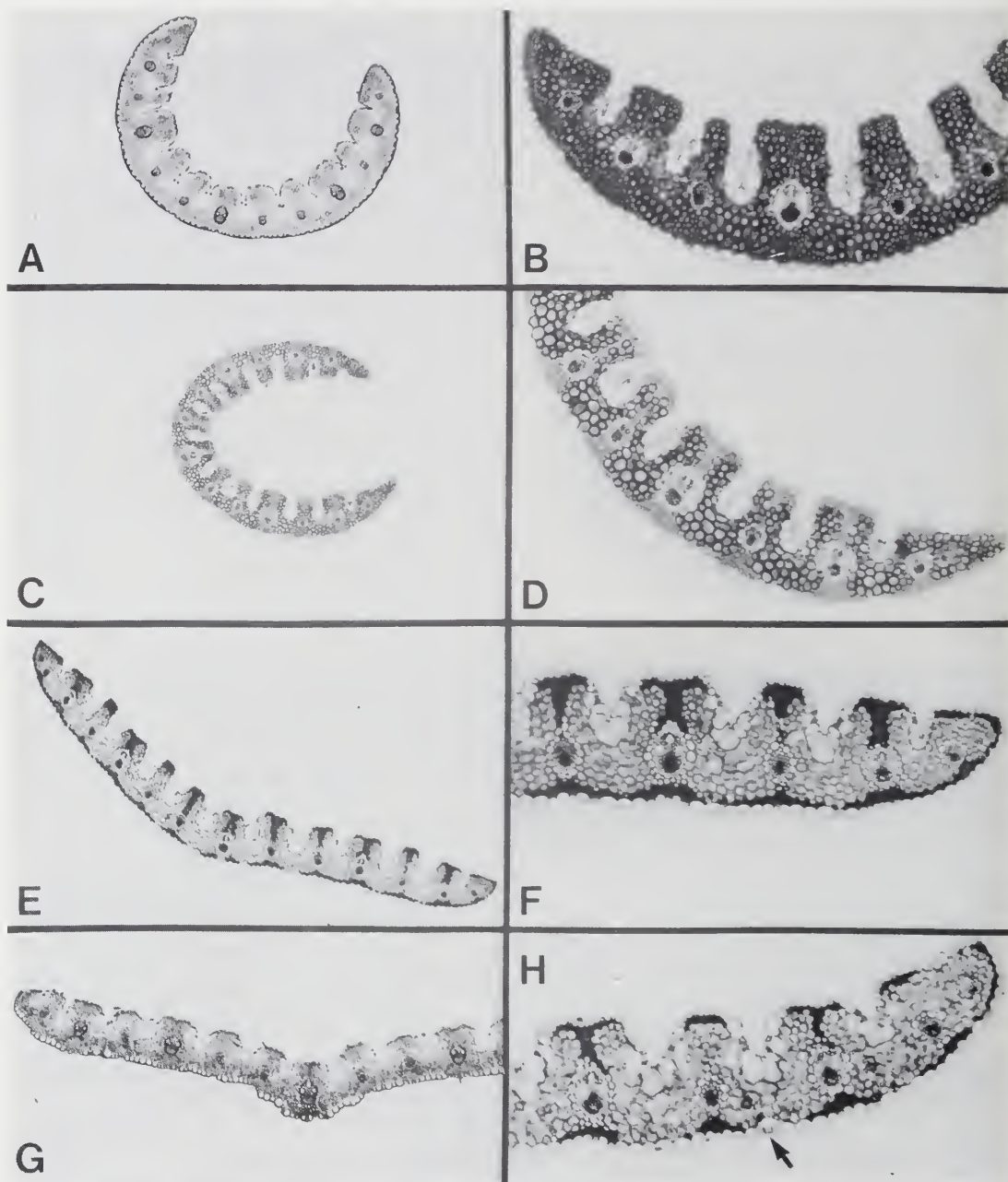


FIGURE 7c.1.—*Pentaschistis pallida* form C 'albescens': transsectional leaf anatomy.

A, narrow, inrolled leaf outline.

B, detail of tapering margin, deep, cleft-like adaxial furrows and flat-topped ribs; note that girders are not comprised of lignified tissue and stain the same colour as the mesophyll.

C, inrolled outline.

D, narrow, pointed margin; note relatively compact nature of the chlorenchyma.

E, open, expanded outline but lamina still narrow.

F, detail of sclerenchyma girders with abaxial girders almost fusing to form continuous hypodermal layer.

G, open leaf of wider lamina.

H, abaxial girders spreading along epidermis but not fused; note stomatal aperture (arrowed).

A, B, *Ellis* 2528; C, D, *Ellis* 2356; E, F, *Ellis* 5475; G, *Ellis* 5452; H, *Ellis* 5476; A, C, E, G, $\times 100$; B, D, F, H, $\times 250$.

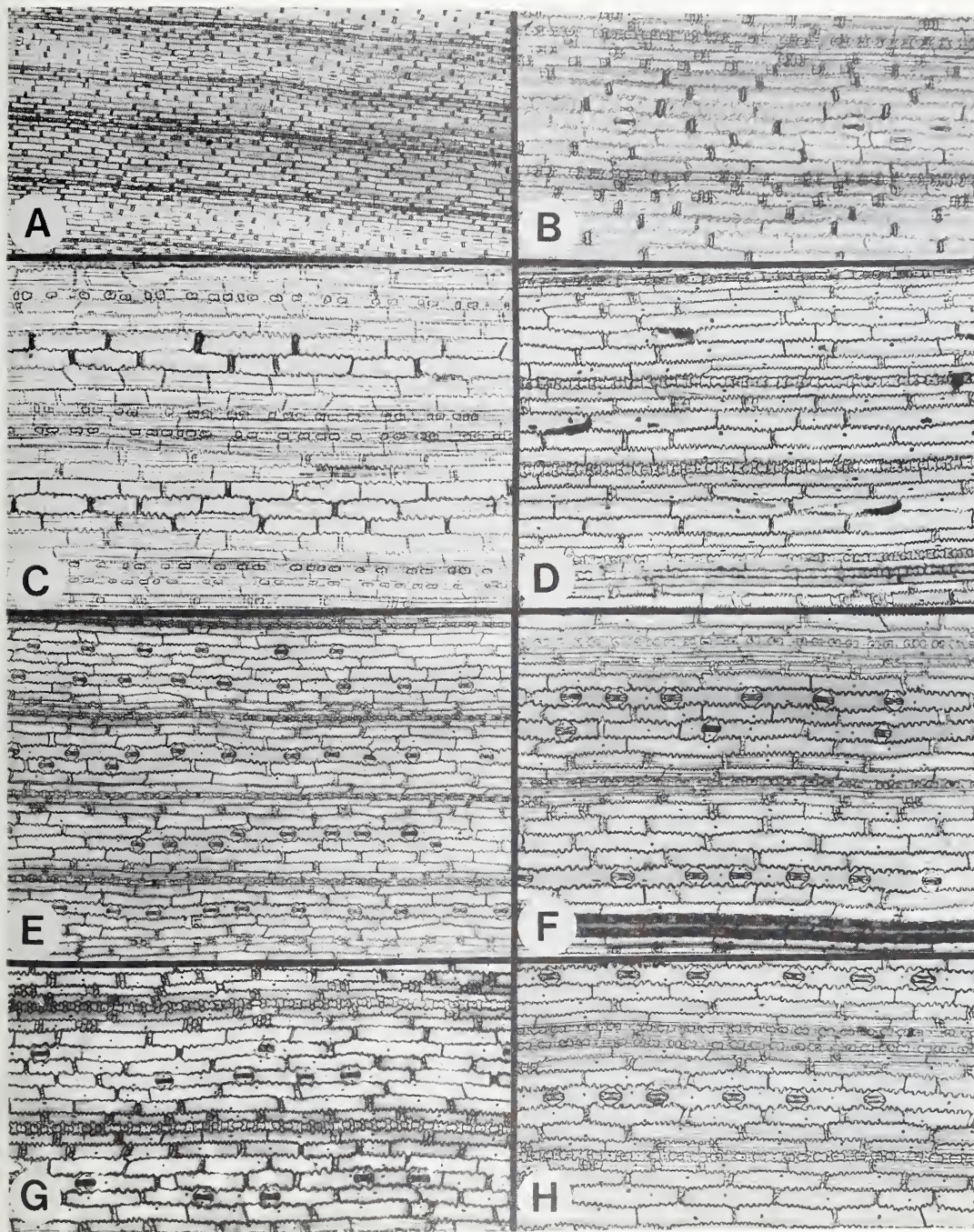


FIGURE 7c.2.—*Pentaschistis pallida* form C 'albescens': abaxial epidermis. A–D, specimens with few or no abaxial stomata. E–H, specimens with stomata.

- A, epidermal zonation with little differentiation between costal and intercostal long cell size and shape.
 B, cell detail with thick-walled long cells separated by tall and narrow cork-silica cell pairs; note few stomata and absence of epidermal appendages; costal silica bodies very irregular in shape.
 C, no stomata or microhairs present.
 D, epidermis of specimen with no stomata but microhairs common.
 E, zonation with intercostal zones with regular stomatal files.
 F, detail of E showing stomata and sinuous-walled long cells; silica bodies very irregular in shape and microhairs absent.
 G, short, sinuous long cells, stomata and unusual costal silica cell files; the silica bodies unusually small.
 H, typical epidermis of this form.
 A, B, *Ellis* 2528; C, *Ellis* 2329; D, *Ellis* 5602; E, F, *Ellis* 5476; G, *Ellis* 5452; H, *Ellis* 5474. A, $\times 100$; E, $\times 160$;
 B, C, D, F, G, H, $\times 250$.

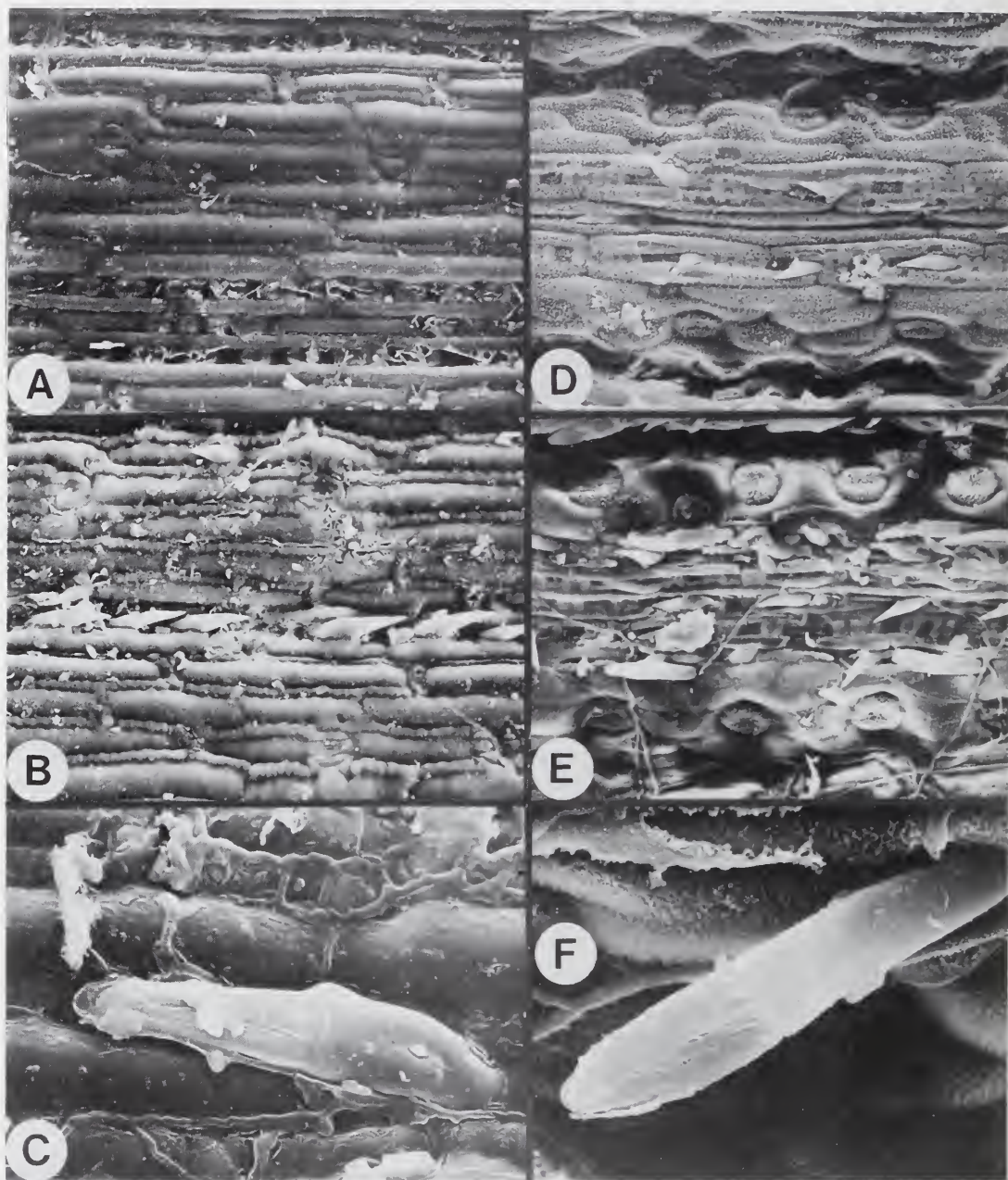


FIGURE 7c.3.—*Pentaschistis pallida* form C 'albescens': leaf blade ultrastructure. A–C, abaxial epidermis. D–F, adaxial epidermis.

A, thick-walled long cells and silica cell files with cork cells sunken below the level of the silica bodies; no epidermal appendages.

B, file of short hooks along costal zone.

C, abaxial microhair with slightly longer distal cell gently tapering; note fungal hyphae on surface of cuticle.

D, adaxial rib with small hooks and stomata located on steep sides of furrows.

E, microhairs, hooks and stomata.

F, adaxial microhair with untapered distal cell; basal cell slightly longer than distal cell.

A, D, *Ellis* 5476; B, E, F, *Ellis* 5452; C, *Ellis* 5602. A, B, D, E, $\times 200$; C, $\times 800$; F, $\times 1000$.

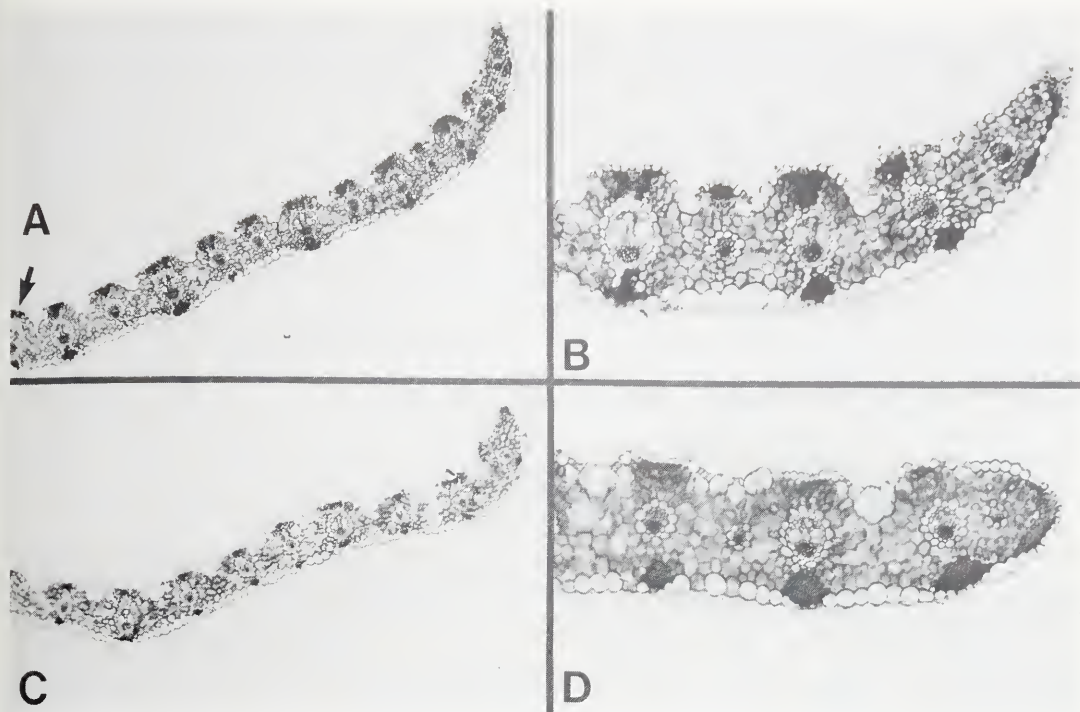


FIGURE 7d.1.—*Pentaschistis pallida* form D 'australis': leaf blade in transverse section.

A, expanded outline but broadly infolded; note undifferentiated median vascular bundle (arrowed); near centre of blade two third order bundles interspaced between the first order bundles but laterally only a single small bundle occurs.

B, detail of tapering leaf margin, girders and strands, and relatively thick cuticle.

C, outline.

D, detail of vascular bundles and very small outer bundle sheath cells, chlorenchyma of large angular cells and sclerenchyma girders and strands; note margin not tapering.

A, B, *Ellis* 5821; C, *Ellis* 5825; D, *Ellis* 5823. A, C, $\times 100$; B, D, $\times 250$.

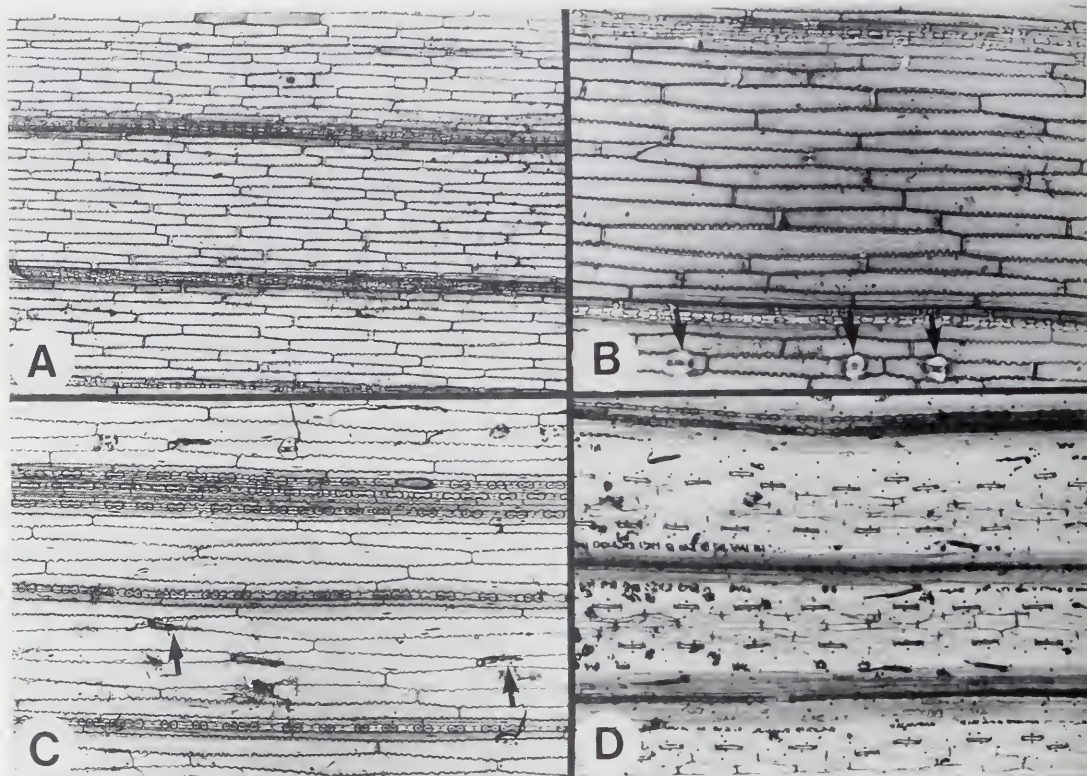


FIGURE 7d.2.—*Pentaschistis pallida* form D 'australis': abaxial and adaxial epidermides. A–C, abaxial epidermis. D, adaxial epidermis.

A, epidermal zonation with clearly differentiated costal and intercostal zones; note narrow costal zones (3 cells wide) and absence of stomata in intercostal zones.

B, detail of fusiform, elongated intercostal long cells with slightly sinuous walls; stomata (arrowed) rare and, when present, often deformed; costal silica bodies very irregular in form and shape but often nodular.

C, fusiform long cells and very few stomata; note presence of microhairs (arrowed) and more uniform dumbbell-shaped to nodular silica bodies.

D, adaxial epidermis with numerous stomata and microhairs and long cells short and not fusiform in shape.

A, B, *Ellis* 5821; C, *Ellis* 5830; D, *Ellis* 5601. A, $\times 160$; B–D, $\times 250$.

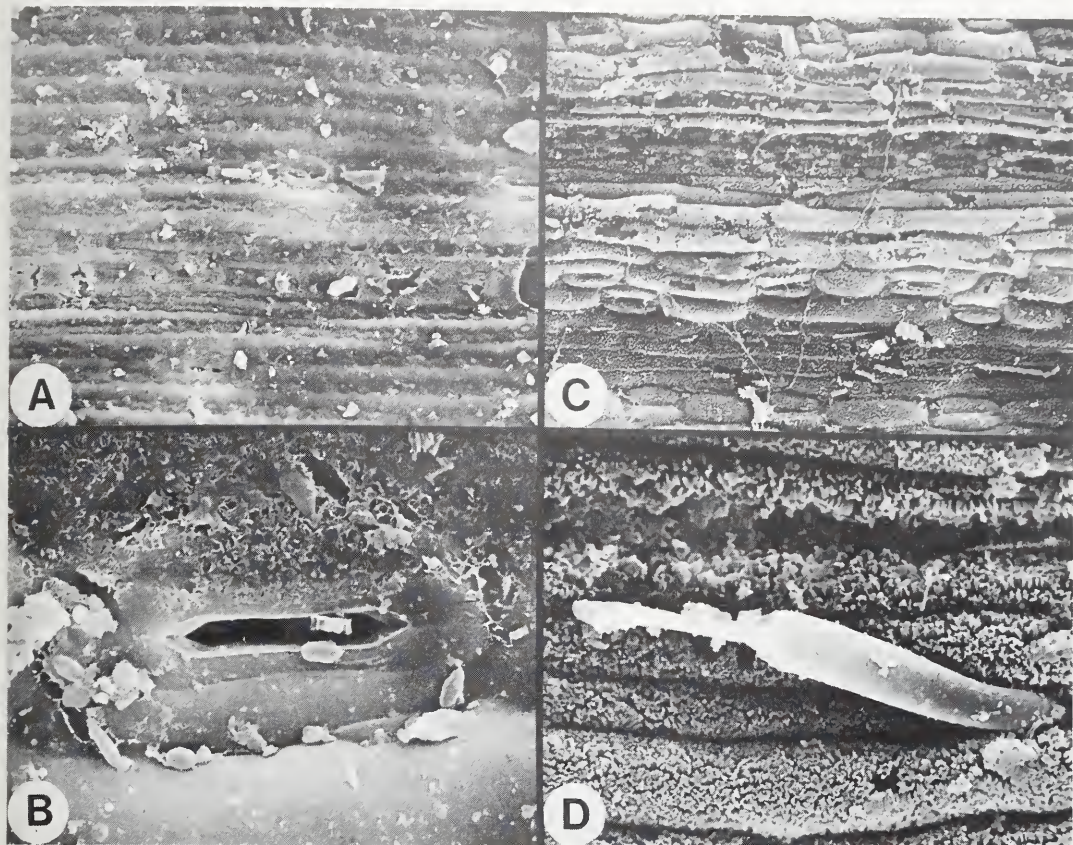


FIGURE 7d.3.—*Pentaschistis pallida* form D 'australis': epidermal ultrastructure. A, B, abaxial epidermis. C, D, adaxial epidermis.

A, featureless epidermis without stomata or microhairs; note thickened walls of fusiform long cells.

B, rare stomatal aperture, flush with the epidermal surface.

C, short adaxial long cells with inflated periclinal walls.

D, finger-like microhair with distal and basal cells about equal in length.

A–D, *Ellis 5601*. A, C, $\times 200$; D, $\times 850$; B, $\times 1300$.

FIGURE 7e.1.—*Pentaschistis pallida* form E 'angustifolia': leaf blade in transverse section and abaxial epidermis.

A–D, leaf transections. E–H, abaxial epidermis.

A, inrolled, narrow leaf section.

B, detail of tapering margin, large girders in association with the first order bundles and only small strands with the smaller bundles; the chlorenchyma cells are relatively large and angular and rather compact.

C, narrow, inrolled leaf blade with reduction in the number of vascular bundles.

D, detail of tapering margin with unstalked marginal gland (arrowed) and large girders subtending the larger vascular bundles.

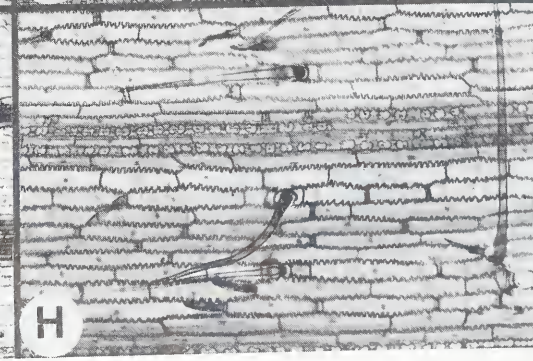
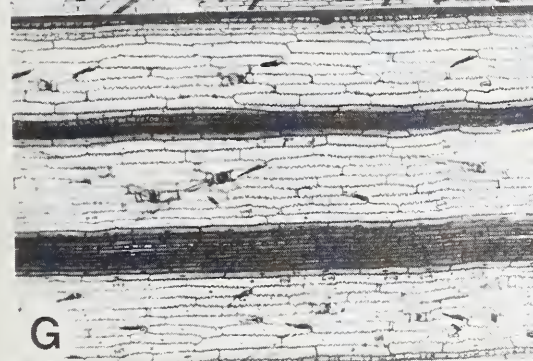
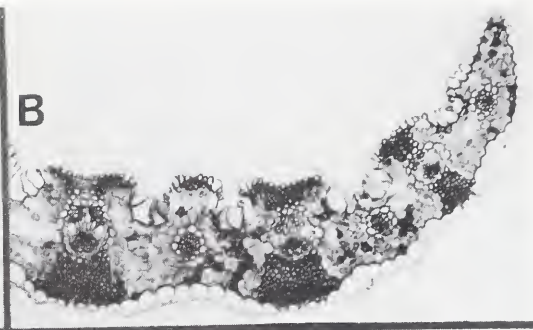
E, lateral part of epidermis showing numerous, small, unstalked marginal glands and elongate macrohairs.

F, detail of macrohair bases with small cushions and microhairs (arrowed); note absence of stomata, short rectangular long cells with sinuous walls separated by a single tall and narrow short cell and dumbbell-shaped silica bodies.

G, epidermal zonation with very few stomata in the intercostal zones and wide costal zones.

H, detail of short, stiff macrohairs with swollen bases inserted between a few specialized epidermal cells; microhairs common and silica bodies variable in shape but of the dumbbell type.

A, B, G, H, *Ellis* 5633; C, D, E, F, *Ellis* 5634. A, C, E, $\times 100$; G, $\times 160$; B, D, F, H, $\times 250$.



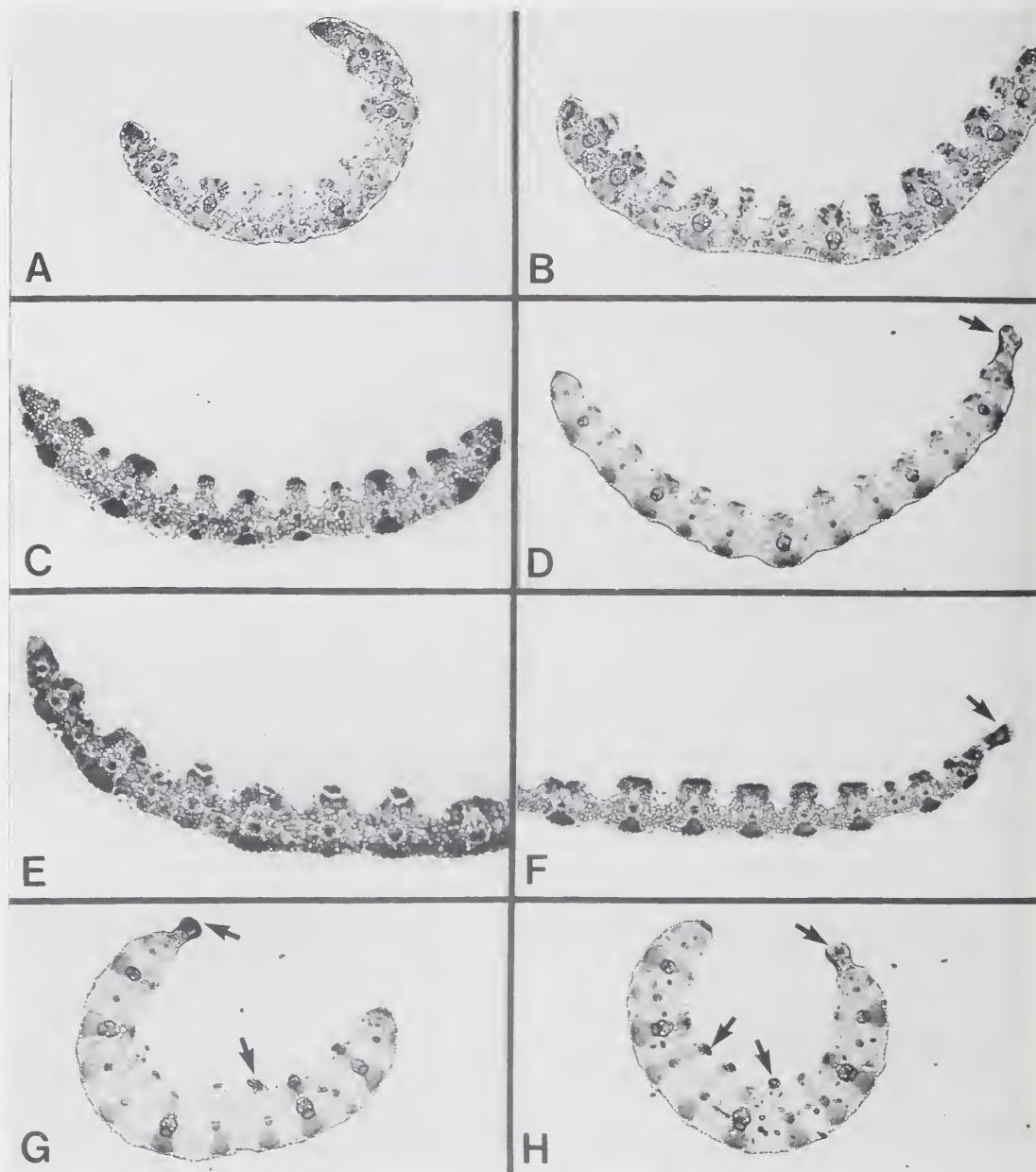


FIGURE 7f.1.—*Pentaschistis pallida* form F 'pillansii': variation in transectional leaf outline of specimens without glands; with marginal glands only; and with marginal and adaxial glands.

- A, narrow, inrolled mesic leaf type without glands or macrohairs.
 B, wider but slightly infolded leaf without glands or macrohairs.
 C, relatively narrow, expanded blade with no glands but with macrohairs without cushion bases.
 D, thinner leaf with marginal gland (arrowed) but with macrohairs without cushions.
 E, broad, expanded leaf without glands but with macrohairs without cushions.
 F, wide, expanded leaf with both glands (arrowed) and macrohairs without cushions.
 G, narrow, inrolled blade with both marginal and adaxial glands (arrowed) and macrohairs without cushions.
 H, narrow, inrolled blade with both marginal and adaxial glands (arrowed) but with few macrohairs.

A, Ellis 2441; B, Ellis 2442; C, Ellis 5780; D, Ellis 5505; E, Ellis 5779; F, Ellis 5482; G, Ellis 5507; H, Ellis 5509.

All $\times 100$.

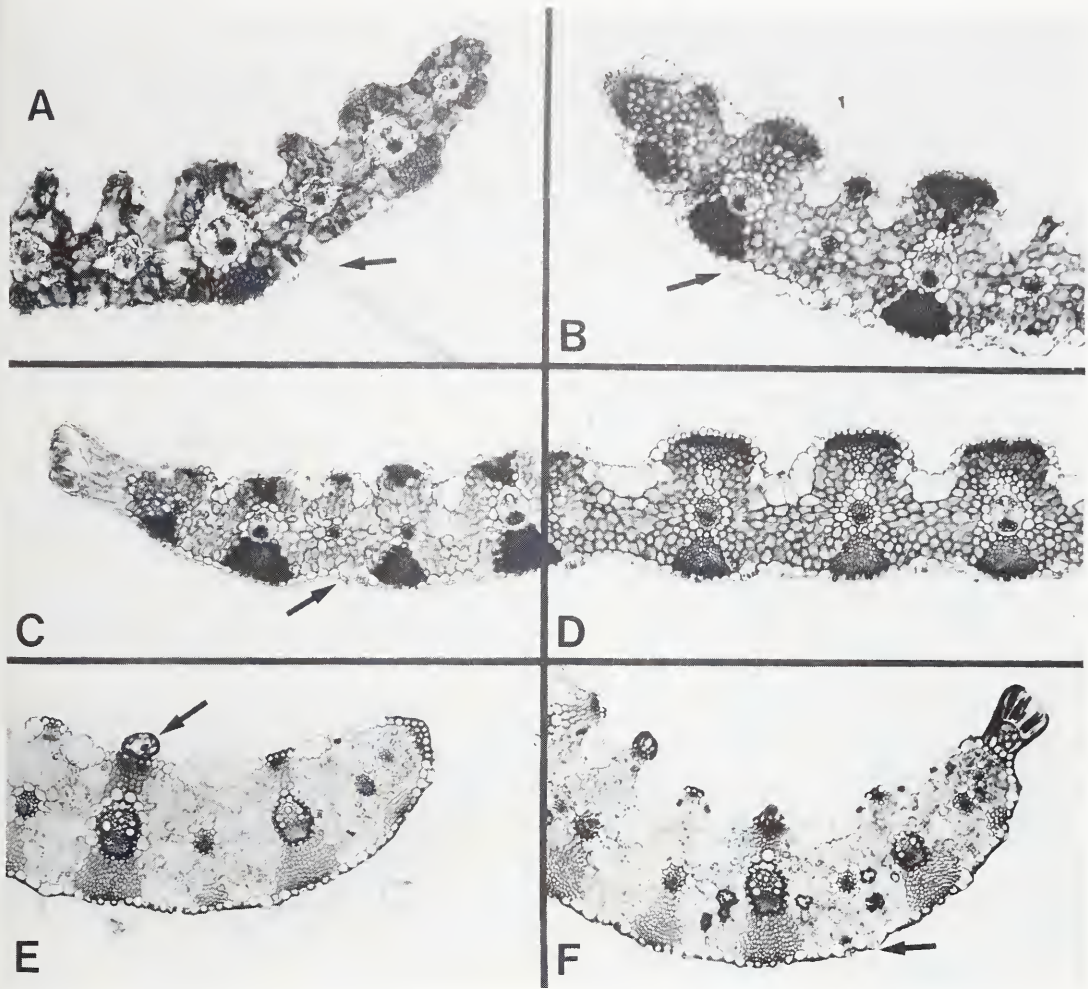


FIGURE 7f.2.—*Pentaschistis pallida* form F 'pillansii': variation in transectional anatomy of specimens without glands; with marginal glands only; and with marginal and adaxial glands.

- A, lateral part of leaf clearly showing macrohair with typical raised cushion basal cells (arrowed).
 B, specimen with macrohairs without cushion bases as seen in section (arrowed).
 C, margin showing stalked marginal gland and basal cells of macrohair (arrowed).
 D, mesic type anatomy although the chlorophyll cells are rather compact and regularly arranged.
 E, specimen with adaxial gland (arrowed); note sectioned base of abaxial macrohair without cushion cells.
 F, specimen with marginal and adaxial glands; note basal cells of macrohairs (arrowed).

A, *Ellis* 2440; B, *Ellis* 5780; C, *Ellis* 5505; D, *Ellis* 5482; E, *Ellis* 5507; F, *Ellis* 5509. All $\times 250$.

FIGURE 7f.3.—*Pentaschistis pallida* form F 'pillansii': abaxial epidermal variation in similar sequence to that illustrated in Figure 7f.1, 7f.2.

- A, lateral part of blade showing absence of marginal glands but long stiff macrohairs with raised cushion bases present.
 - B, no macrohairs or glands; note hexagonal shape of long cells and irregularly dumbbell-shaped silica bodies.
 - C, lateral part of blade showing marginal glands and flexible, thin macrohairs with few specialized basal cells.
 - D, epidermal detail of specimen with glands and macrohairs; note single inflated epidermal cell associated with the base of the thin, flexible macrohairs which swell slightly at the base; long cells shortly rectangular with very sinuous walls; wide costal zones with very uniform silica bodies.
 - E, epidermal pattern of specimen with marginal and adaxial glands; costal and intercostal zones clearly differentiated, many long, flexible macrohairs and microhairs (arrowed) present.
 - F, detail of flexible macrohairs with their swollen bases inserted on one side of an inflated epidermal cell; note extremely long microhairs (at least $3\times$ the length of the stomata).
 - G, epidermis of specimen with adaxial glands showing short, rather hexagonal long cells and very short macrohairs with inflated epidermal cell associated with the base.
 - H, specimen with hexagonal intercostal long cells and short macrohairs paired with an inflated epidermal cell; this specimen appears to be without both marginal and adaxial glands.
- A, *Ellis* 2440; B, *Ellis* 2442; C, *Ellis* 5482; D, *Ellis* 5481; E, F, *Ellis* 5507; G, *Ellis* 5420; H, *Ellis* 5779. A, C, E, $\times 160$; B, D, G, H, $\times 250$; F, $\times 400$.

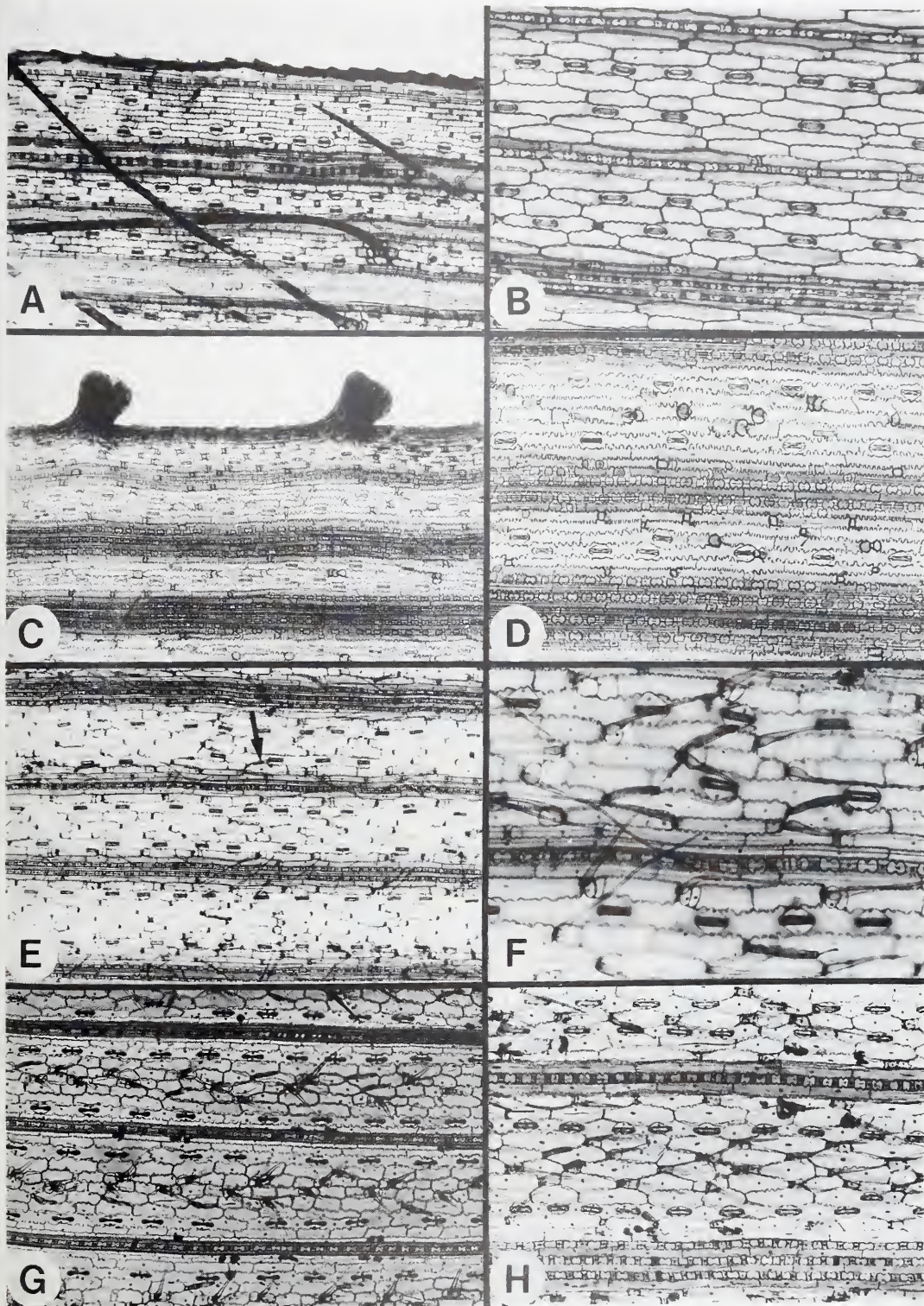


FIGURE 7f.4.—*Pentascistis pallida* form F 'pillansii': epidermal ultrastructure. A–D, abaxial epidermis. E–H, adaxial epidermis.

A, flexible type macrohair with swollen base but without raised cushion cells; note dumbbell-shaped silica bodies.

B, abaxial microhair with distal and basal cells equal in length.

C, prickles and bases of macrohairs (the hairs having fallen out).

D, detail of very short macrohair inserted between a few swollen epidermal cells.

E, adaxial surface with thin, flexible macrohairs and costal prickles; no adaxial glands present.

F, stalked marginal gland.

G, adaxial surface with macrohairs, prickles and costally situated glands.

H, detail of dome-shaped adaxial gland on which cell outlines are not visible.

A, B, E, F, *Ellis* 5482; C, D, G, H, *Ellis* 5420. E, G, $\times 210$; C, $\times 270$; A, F, $\times 380$; H, $\times 700$; D, $\times 850$; B, $\times 1150$.

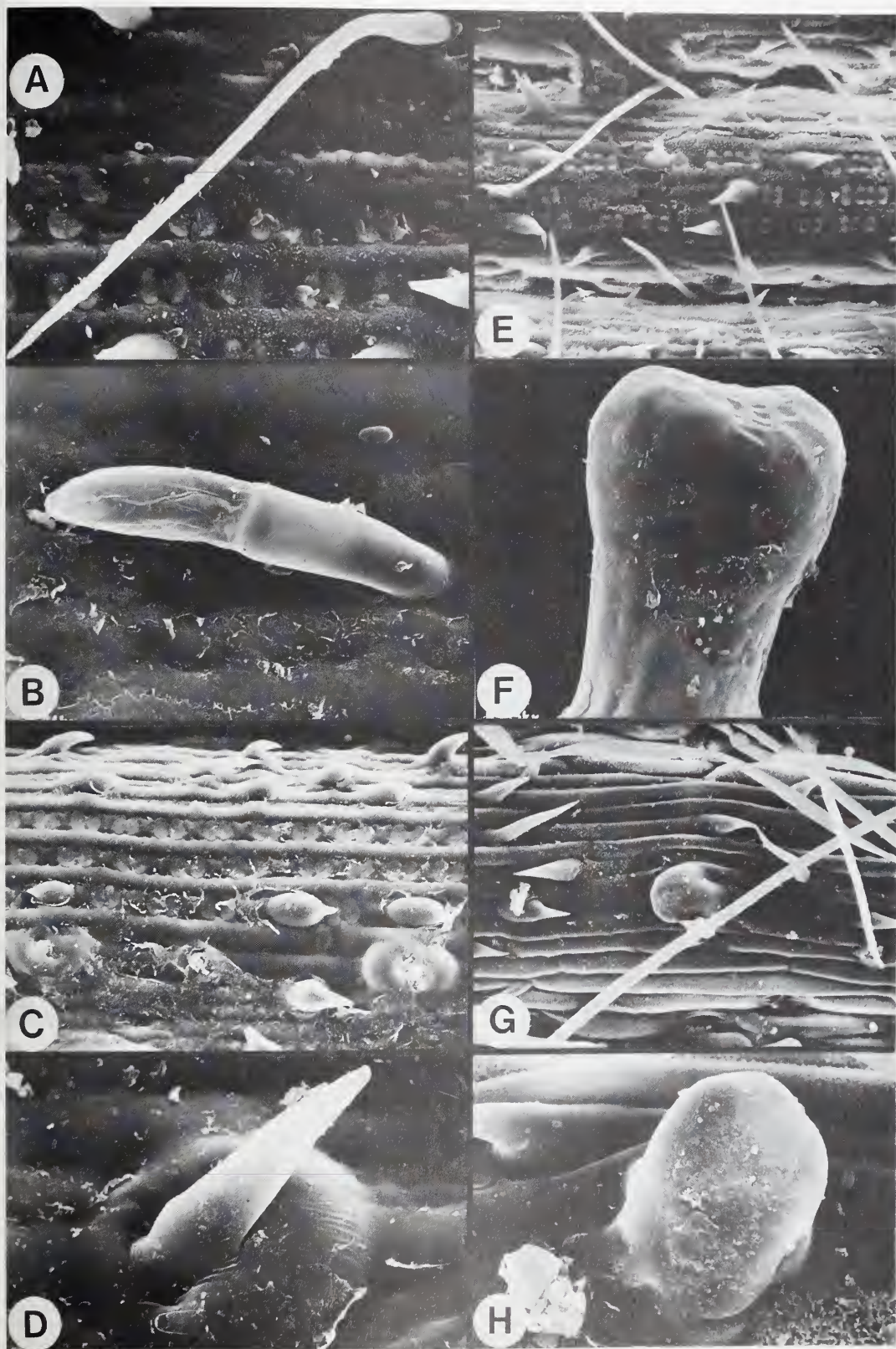


FIGURE 7f.5.—*Pentascistis pallida* form F 'pillansii': anatomy of specimen which resembles *P. rupestris* closely in leaf anatomy. A, B, leaf in transection. C, D, abaxial epidermis; E–H, ultrastructure.

A, inrolled leaf type but with tissue configuration very similar to that of some specimens of *P. rupestris*.

B, detail of margin showing stalked, marginal gland.

C, epidermal zonation with costal zones up to 7 cell files wide.

D, detail of short, very irregular silica bodies of the dumbbell type; rectangular long cells with thick, sinuous walls and variable stomata, some being almost triangular in shape; note that some of the microhairs are tricellular (arrowed).

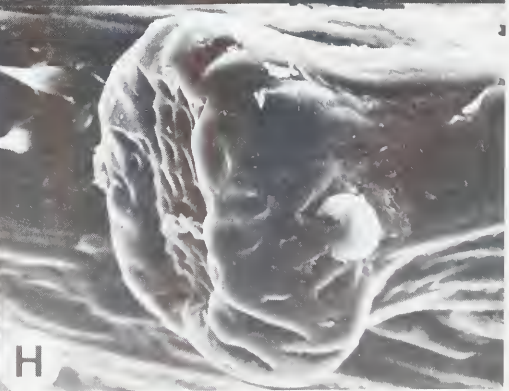
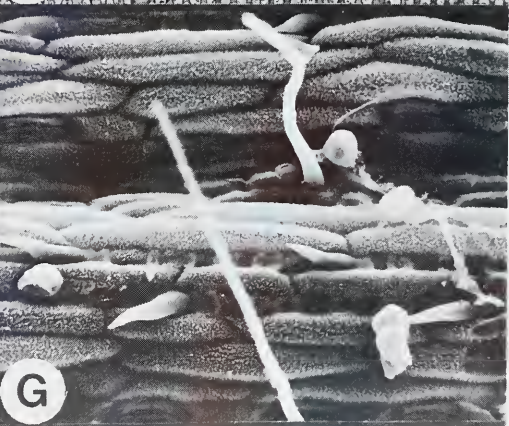
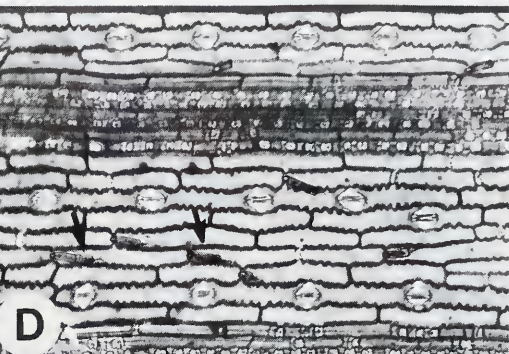
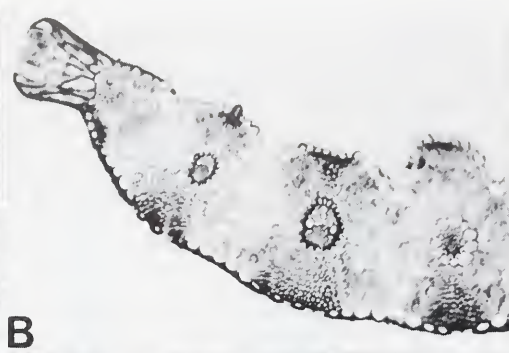
E, abaxial surface showing very thick cuticle, prickles and microhairs.

F, detail of bicellular abaxial microhair.

G, adaxial epidermis with soft, flexible macrohairs and prickles.

H, stalked marginal gland.

A–H, *Ellis* 5588. A, $\times 100$; C, $\times 160$; E, G, $\times 200$; B, D, $\times 250$; H, $\times 330$; F, $\times 1320$.



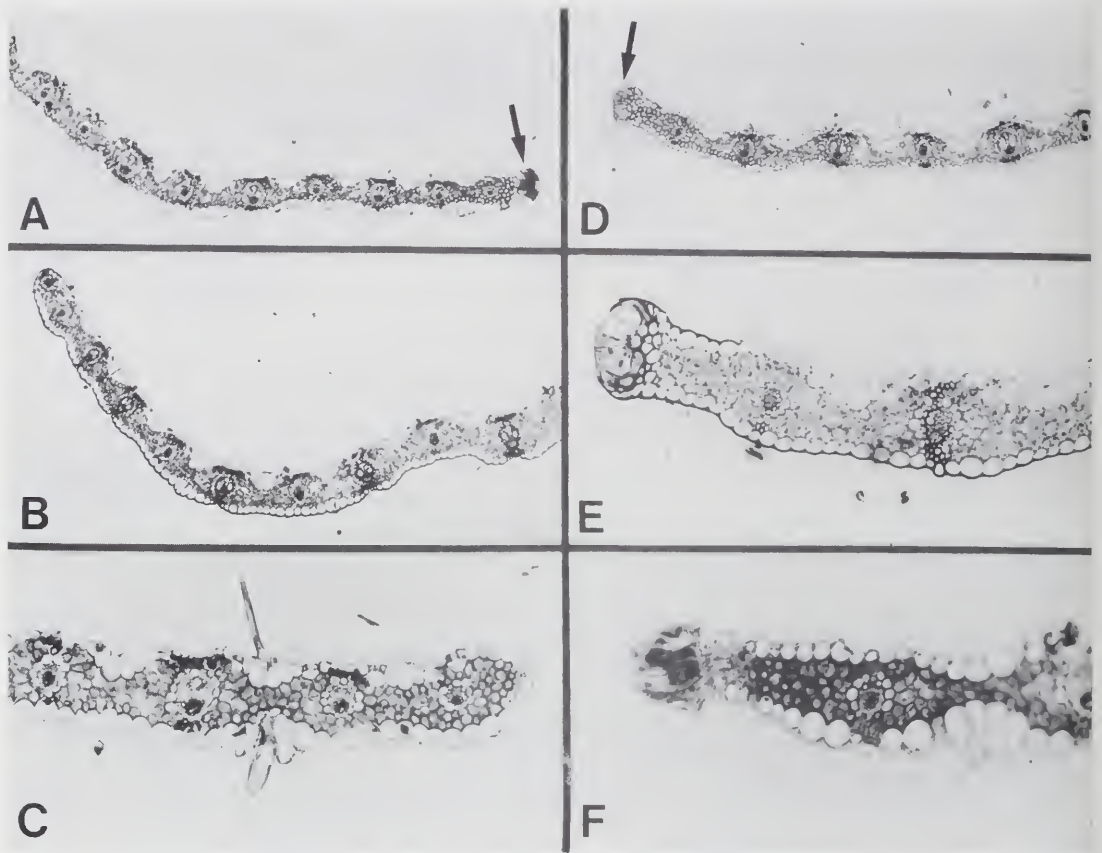


FIGURE 7g.1.—*Pentaschistis pallida* form G 'silvatica': transectional leaf anatomy.

A, very wide thin leaf showing margin with short-stalked marginal gland (arrowed).

B, other half of same lamina as that illustrated in A; no marginal gland evident.

C, detail of margin showing mesic type anatomy, large abaxial epidermal cells and macrohairs with constricted bases embedded between raised cushion cells.

D, lateral part of blade with gland on margin (arrowed).

E, detail of gland showing subglandular cells which are not elongated to form a stalk; gland not clavate.

F, detail of marginal gland with unusually elongated gland cells with collar cells much shorter and subglandular cells not elongated.

A–C, *Ellis 5819*; D, E, *Ellis 5599*; F, *Ellis 5820*. A, B, D, $\times 100$; C, E, $\times 250$; F, $\times 400$.

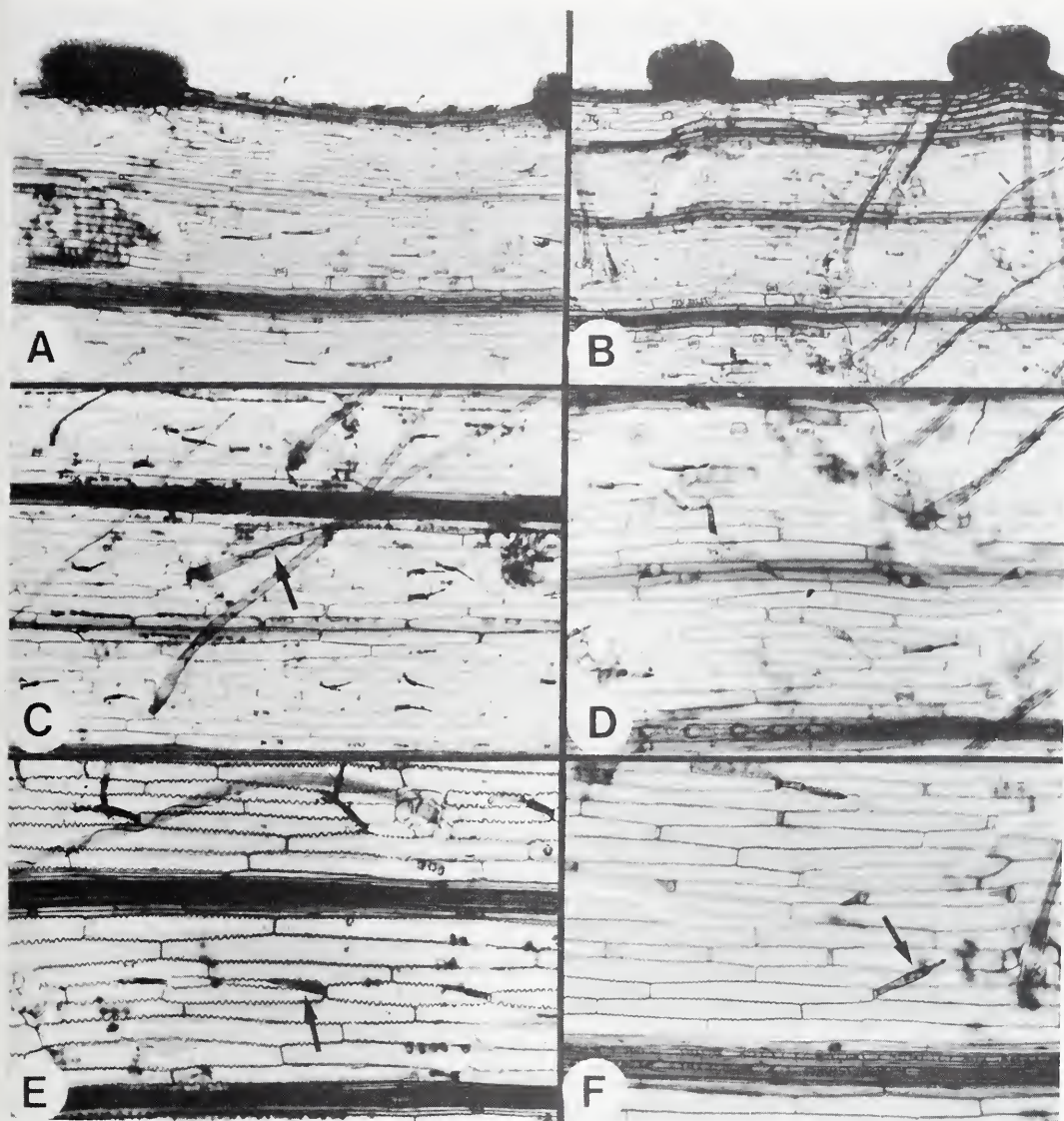


FIGURE 7g.2.—*Pentaschistis pallida* form G 'silvatica': abaxial epidermis in surface view.

A, margin showing horizontally elongated nature of marginal gland which is not clavate or raised on a long stalk.

B, lateral part of lamina with marginal glands and macrohairs.

C, epidermal zonation clearly evident with very narrow costal zones; note very long macrohairs with constricted bases; fungal hyphae present on these hairs (arrowed).

D, more detail of macrohair bases and fungi; note very small prickles on costal zones and prominent microhairs.

E, detail of elongated intercostal long cells with slightly fusiform shape and sinuous walls; stomata not present; note microhairs (arrowed) and fungi on macrohair.

F, detail of macrohair base showing constriction and cushion cells; elongated long cells and no stomata; note microhair consisting of three cells (arrowed).

A, F, *Ellis* 5599; B, D, *Ellis* 5820; C, *Ellis* 5819; E, *Ellis* 5831. A–C, $\times 160$; D–F, $\times 250$.

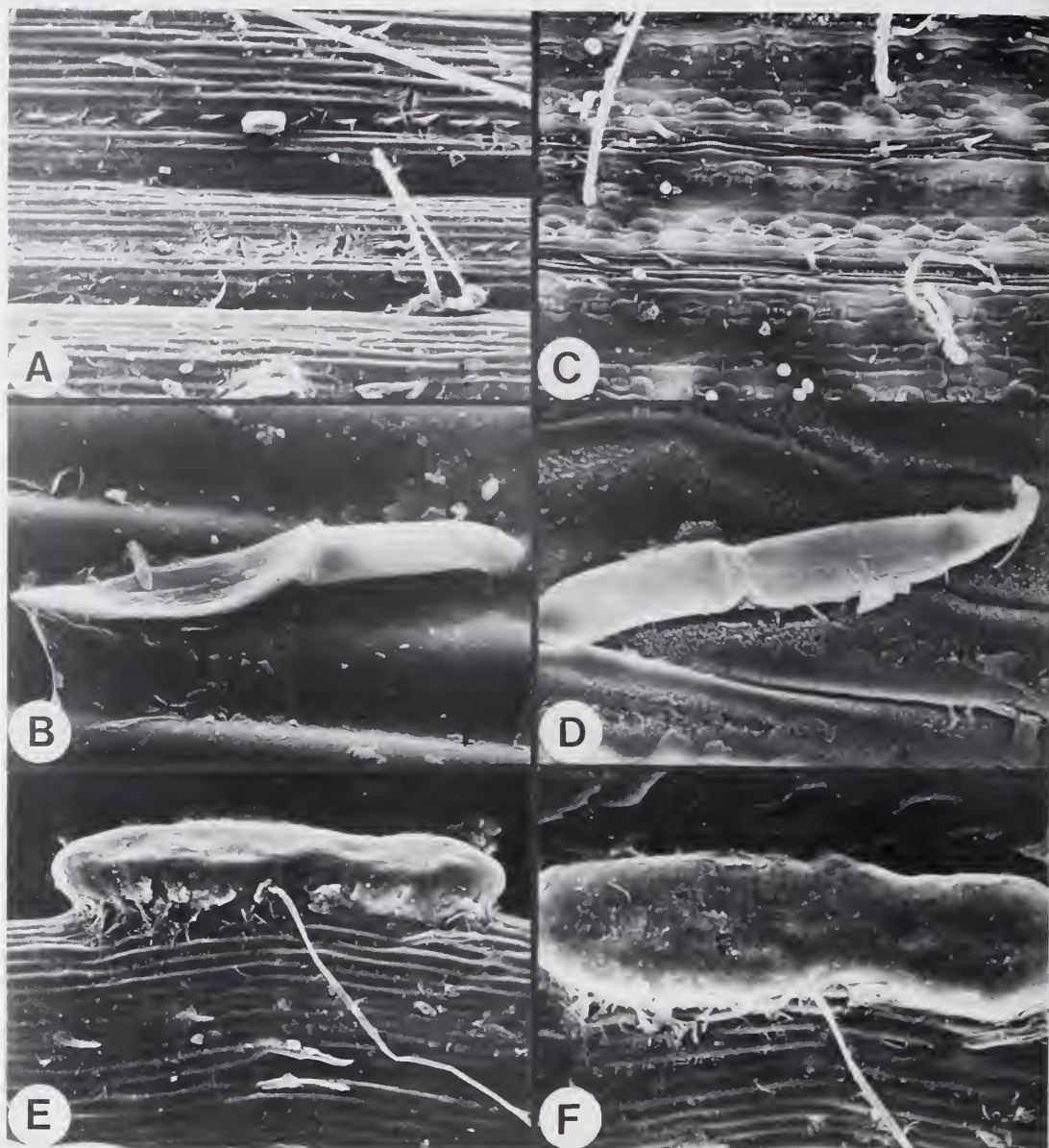


FIGURE 7g.3.—*Pentaschistis pallida* form G 'silvatica': epidermal ultrastructure.
 A, abaxial epidermal pattern with macrohair inserted into raised cushion base.
 B, bicellular abaxial microhair with tapering distal cell equal in length to basal cell.
 C, adaxial epidermis with macrohairs and slightly inflated interstomatal long cells.
 D, adaxial microhair very similar in form to abaxial hair in B but size differs.
 E, profile of slightly raised but elongated marginal gland.
 F, surface view of elongated marginal gland with very small isodiametric gland cells visible.
 A–F, *Ellis 5599*. A, C, $\times 70$; E, F, $\times 100$; B, $\times 550$; D, $\times 800$.

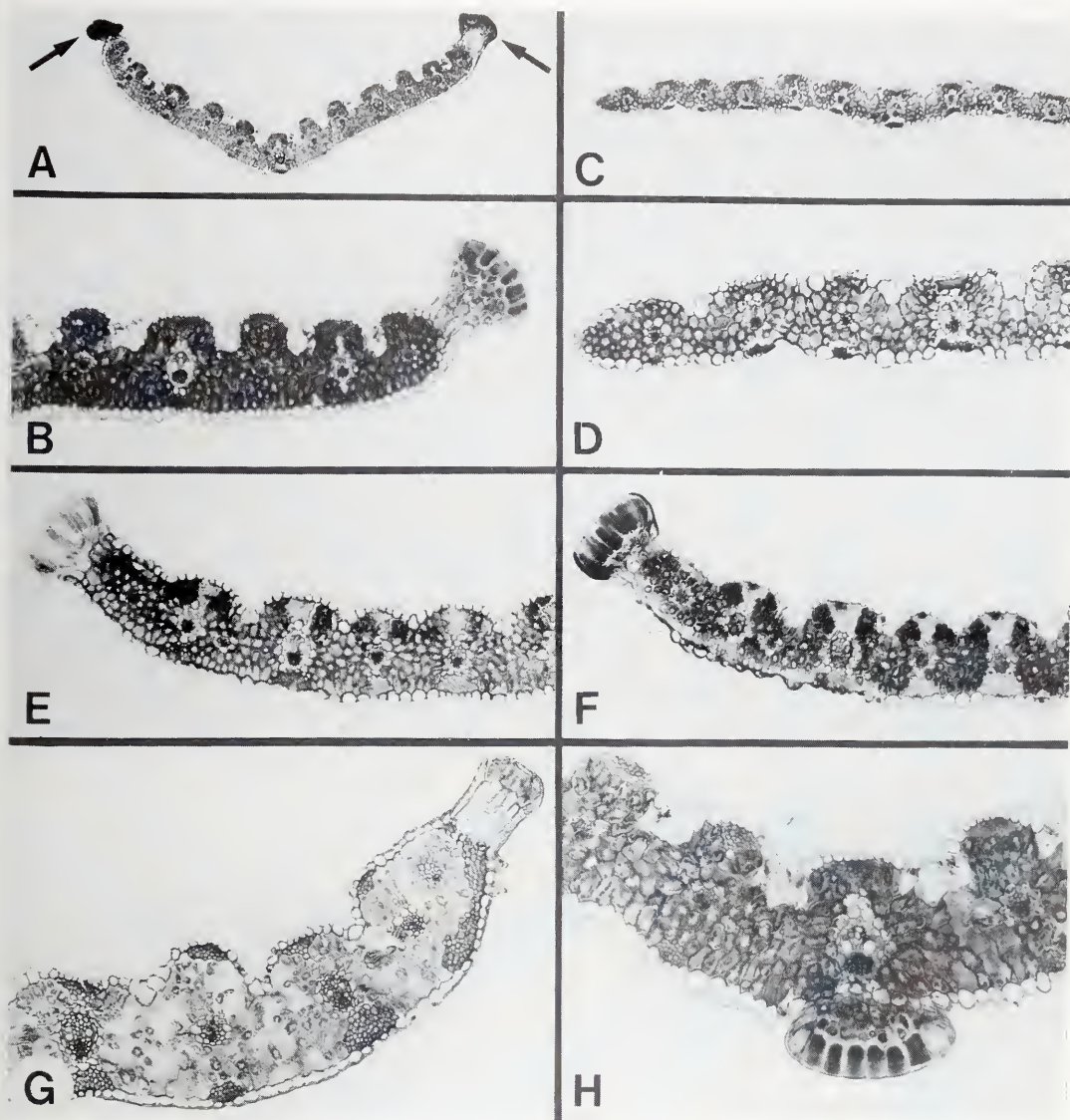


FIGURE 8.1.—*Pentaschistis densifolia*: leaf blade anatomy as seen in transverse section.

A, broadly V-shaped outline; note conspicuous glands on both margins (arrowed).

B, detail of A showing adaxial ribs and steep furrows, rather compact mesophyll tissue and stalked clavate marginal gland.

C, more mesic specimen from shady habitat showing wider but thinner leaf blade.

D, detail of C with ribs and furrows only slightly developed and epidermal cells inflated with very thin cuticle.

E, marginal stalked gland showing regular, elongated gland cells and short subglandular cells; red filter.

F, same as E but taken with a green filter to highlight all red staining tissue; note thick cuticle and dark staining of the collar cells; note that the relatively well-developed sclerenchyma girders are not lignified and don't stain red with safranin but the secondary wall thickening is cellulose.

G, stalked marginal gland. H, short-stalked clavate gland located on the median vascular bundle.

A, B, H, *Ellis* 2493; C, D, *Ellis* 5527; E, F, *Ellis* 5559; G, *Ellis* 5621. A, C, $\times 100$; B, D, E, F, G, $\times 250$; H, $\times 400$.

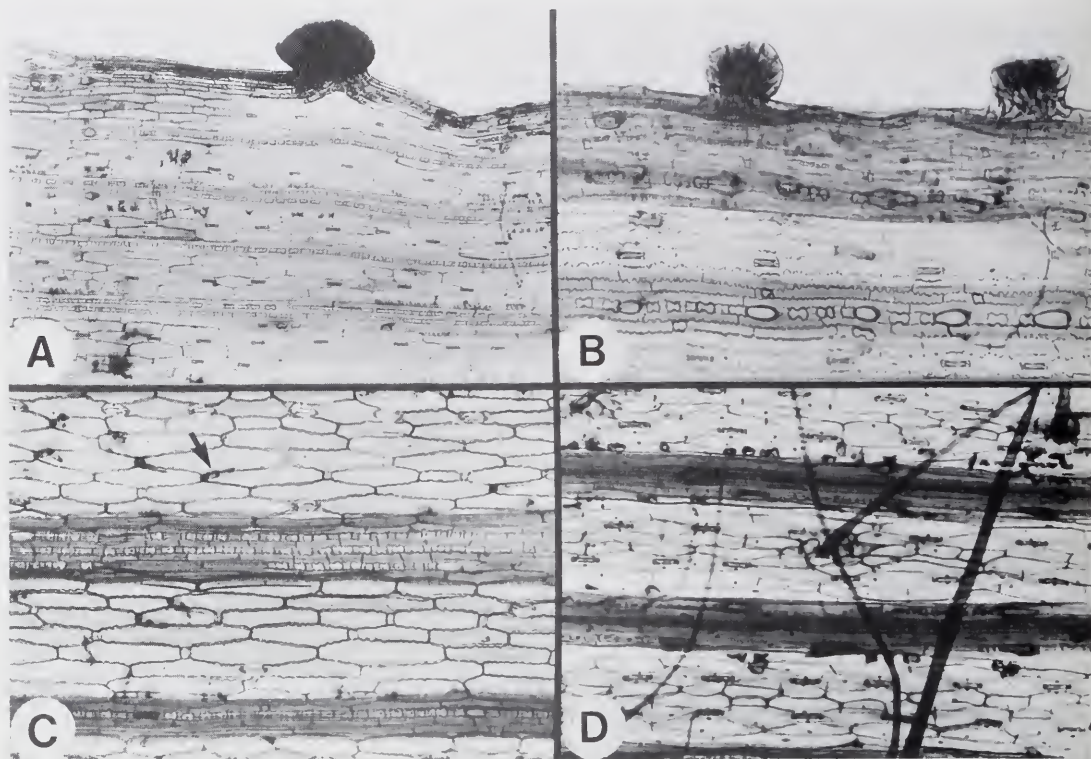
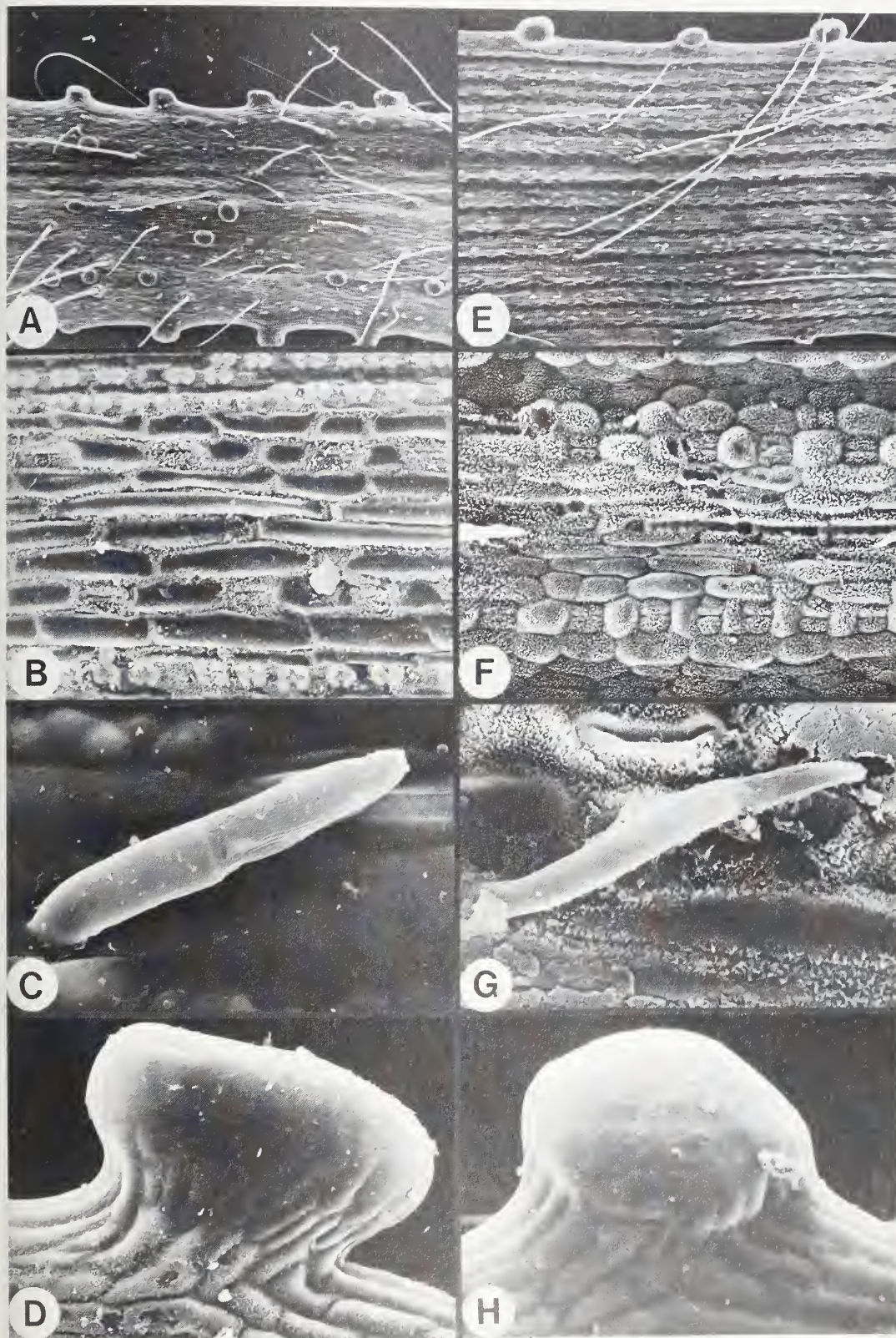


FIGURE 8.2.—*Pentaschistis densifolia*: abaxial epidermis.

- A, margin showing stalked marginal gland; note absence of macrohairs and hexagonal long cell shape; soft, thin-leaved specimen from shady habitat.
 B, marginal stalked glands but note thickened tissue in margin and rectangular long cells; specimen from high altitude, full sun locality.
 C, hexagonal long cells, stomata and small microhairs (arrowed); costal zones relatively wide (5–7 files); specimen from full sun locality.
 D, abaxial macrohairs with cushion bases; hexagonal long cells; shady habitat in moss mat.
 A, Ellis 5527; B, Ellis 5621; C, Ellis 5519; D, Ellis 5584. A, $\times 160$; B–D, $\times 250$.

FIGURE 8.3.—*Pentaschistis densifolia*: SEM of abaxial and adaxial epidermides. A–D, abaxial epidermis. E–H, adaxial epidermis.

- A, lower leaf surface with marginal and costal clavate glands and macrohairs.
 B, hexagonal long cells with inflated periclinal walls; dumbbell-shaped costal silica bodies.
 C, finger-like microhair consisting of two equal length cells. D, profile of clavate marginal gland.
 E, upper leaf surface with marginal glands only and very long macrohairs; compare scale and structure with A.
 F, adaxial epidermis with short but inflated long cells.
 G, adaxial microhair with distal cell tapering and shorter than the basal cell.
 H, profile of marginal gland showing clavate, convex apex.
 A, E, H, Ellis 5584; B, D, F, Ellis 5559; C, Ellis 5519; G, Ellis 6521. A, E, $\times 20$; B, F, $\times 200$; H, $\times 270$; D, $\times 300$; G, $\times 640$; C, $\times 1000$.



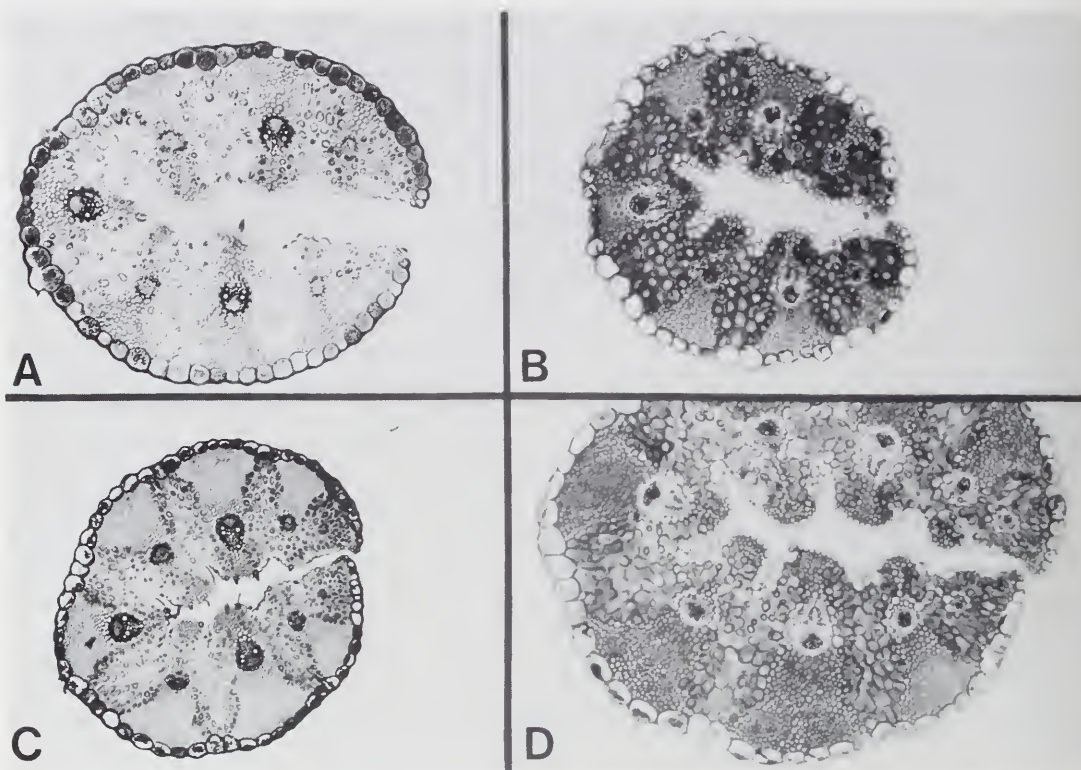


FIGURE 9.1.—*Pentaschistis cirrhulosa*: leaf blade transections.

- A, acicular, permanently infolded outline with no adaxial bulliform cells; abaxial epidermal cells much larger than the adaxial epidermal cells; note darkly staining tannin-like contents of these cells.
 B, acicular outline with abaxial epidermal cells conspicuous, particularly those lying over the intercostal zones; note prominent abaxial sclerenchyma girders.
 C, permanently inrolled leaf blade.
 D, detail showing diffuse type of chlorenchyma with large parenchyma cells; note wide trapezoidal abaxial girders and dark, granular contents of the abaxial epidermal cells which are much larger than the adaxial epidermal cells.
 A, Ellis 4664; B, Ellis 2531; C, D, Ellis 2524. C, $\times 160$; A, B, D, $\times 250$.

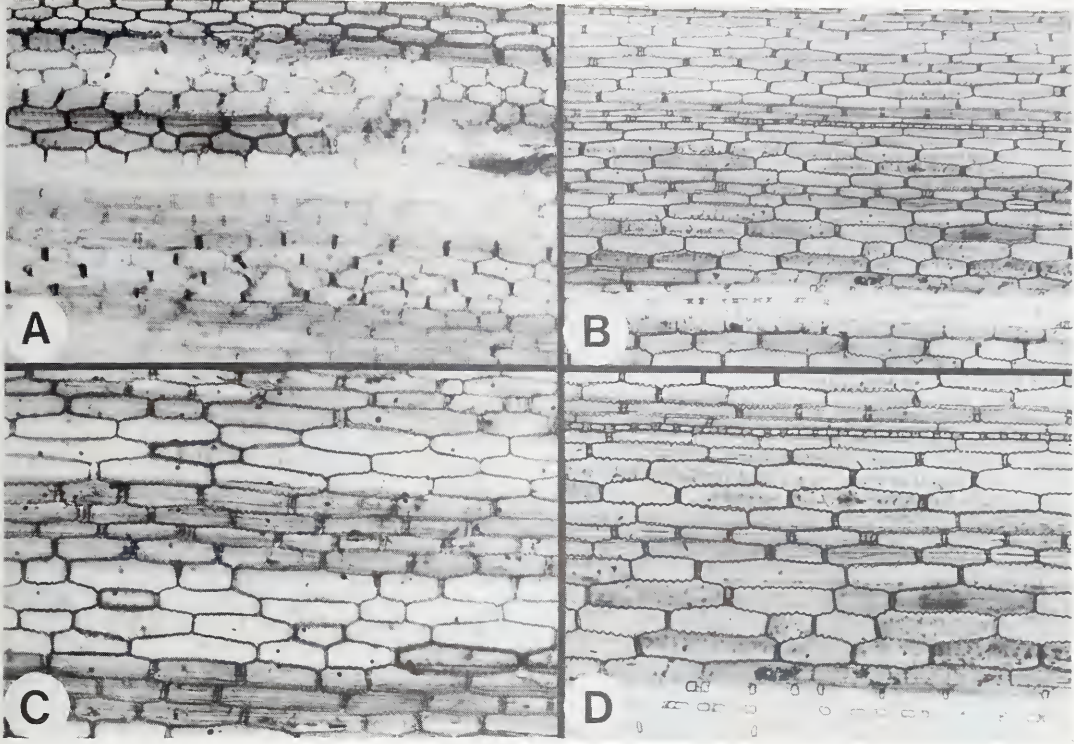


FIGURE 9.2.—*Pentaschistis cirrhulosa*: abaxial epidermal structure.

A, epidermal zonation with costal and intercostal zones poorly differentiated.

B, epidermal pattern with costal zones and intercostal zones distinguishable; this zonation can be inferred from the leaf transection (Figure 9.1B) where the epidermal cells overlying the girders are smaller than those between them.

C, costal and intercostal cells of similar structure but costal zones distinguishable due to darkly staining underlying fibres; all long cells are short and hexagonal in shape and adjoin one another or are separated by tall and narrow short cells; note complete absence of abaxial stomata and epidermal appendages.

D, zonation evident; intercostal long cells short, hexagonal with slightly sinuous walls; no stomata or hairs; silica bodies very variable in shape.

A, *Ellis* 2524; B, D, *Ellis* 2531; C, *Ellis* 4664. A, B, $\times 160$; C, D, $\times 250$.

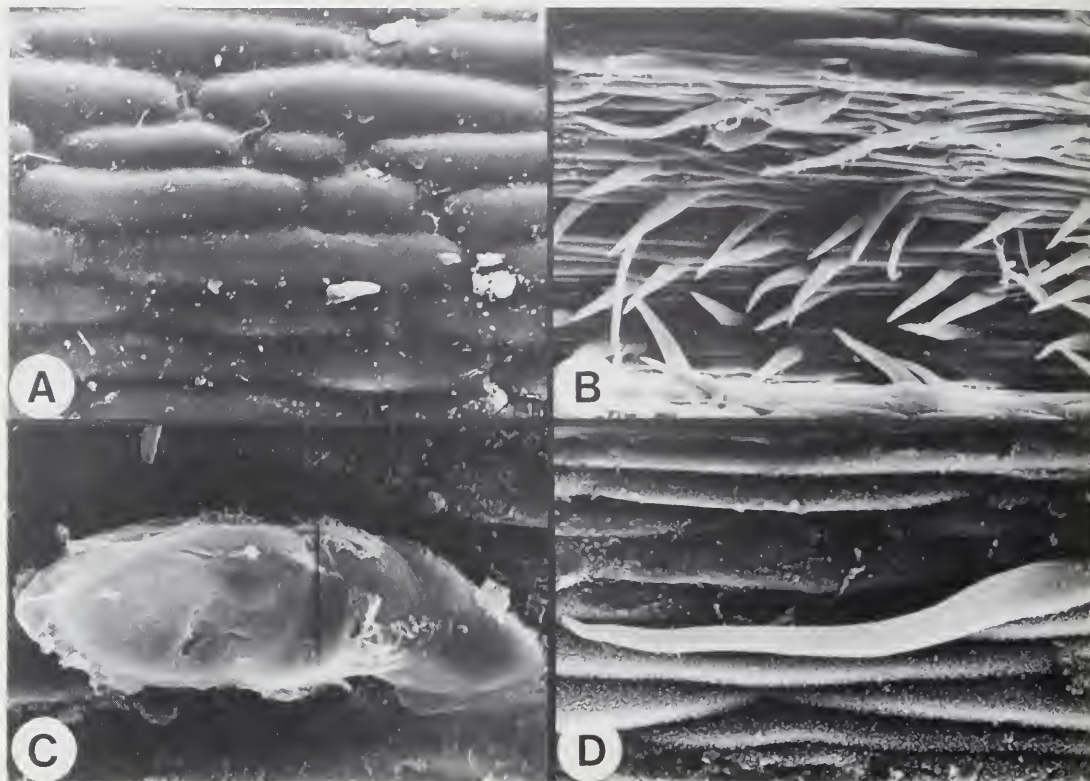


FIGURE 9.3.—*Pentaschistis cirrhulosa*: leaf blade ultrastructure.

A, abaxial surface showing short, inflated long cells; note absence of stomata, microhairs, macrohairs and prickles.

B, adaxial surface with costal prickles; stomata and microhairs located in the grooves.

C, rare, small adaxial microhair with distal cell inflated; resembles the chloridoid type.

D, adaxial prickly hair which tends towards a macrohair in structure.

A–D, *Ellis 4664*. A, B, $\times 200$; D, $\times 570$; C, $\times 1330$.

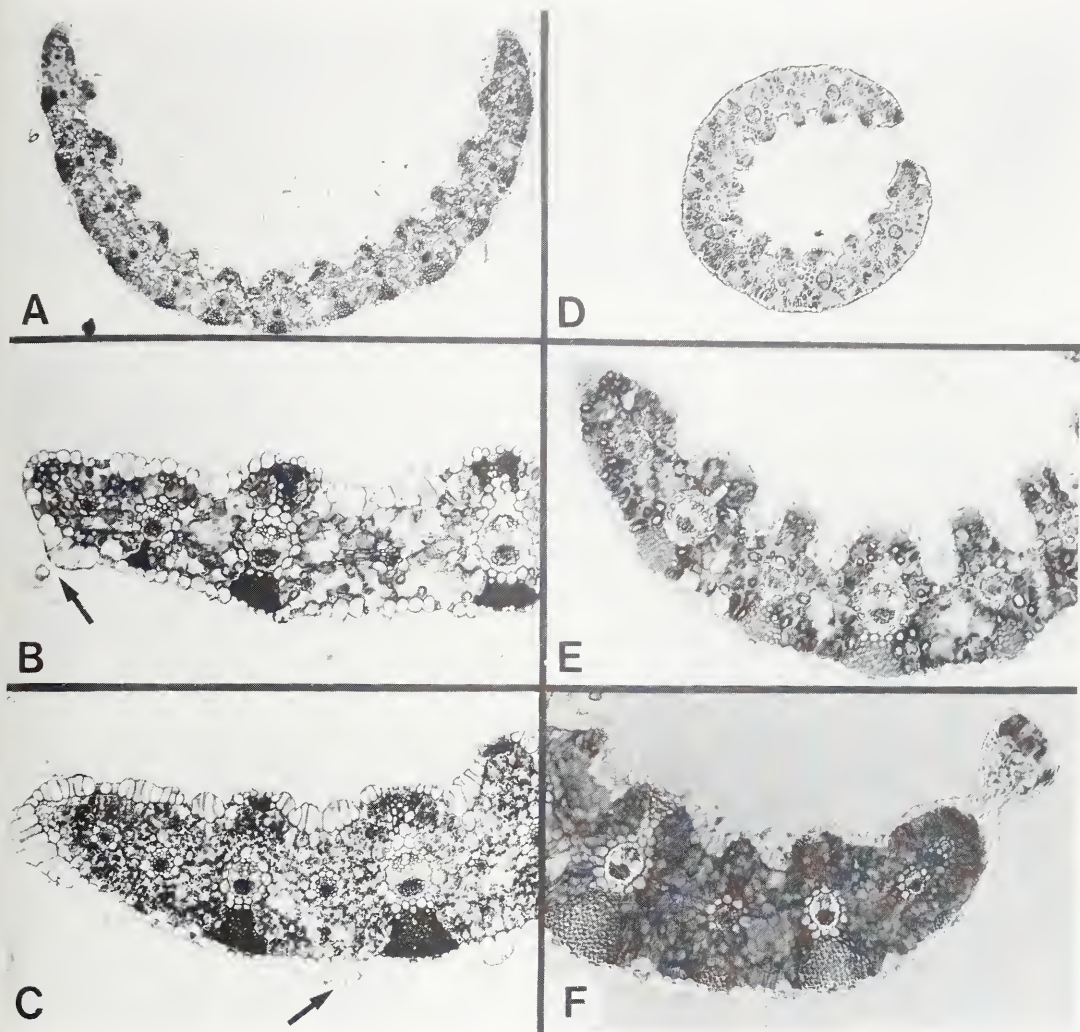


FIGURE 10.1.—*Pentaschistis tomentella*: transsectional leaf anatomy of specimens without adaxial glands. A–C, rather open, soft, flaccid leaves. D–F, inrolled, more rigid leaf type.

A, broadly U-shaped leaf outline.

B, lateral part of blade showing absence of thick cuticle, macrohair base (arrowed) and very diffuse chlorenchyma.

C, margin with slight ribs and shallow furrows, epidermis without conspicuous cuticle, macrohair bases (arrowed) and diffuse mesophyll.

D, tightly inrolled, narrow leaf blade.

E, detail showing cuticle on abaxial epidermal cells in particular; note abaxial girders associated with all vascular bundles and adaxial ribs and furrows.

F, marginal stalked gland and abaxial epidermis with a distinct cuticle developed; note sectioned adaxial macrohairs.

A, *Ellis* 5774; B, *Ellis* 5392; C, *Ellis* 5080; D, E, *Ellis* 2458; F, *Ellis* 2144. A, D, $\times 100$; B, C, E, F, $\times 250$.

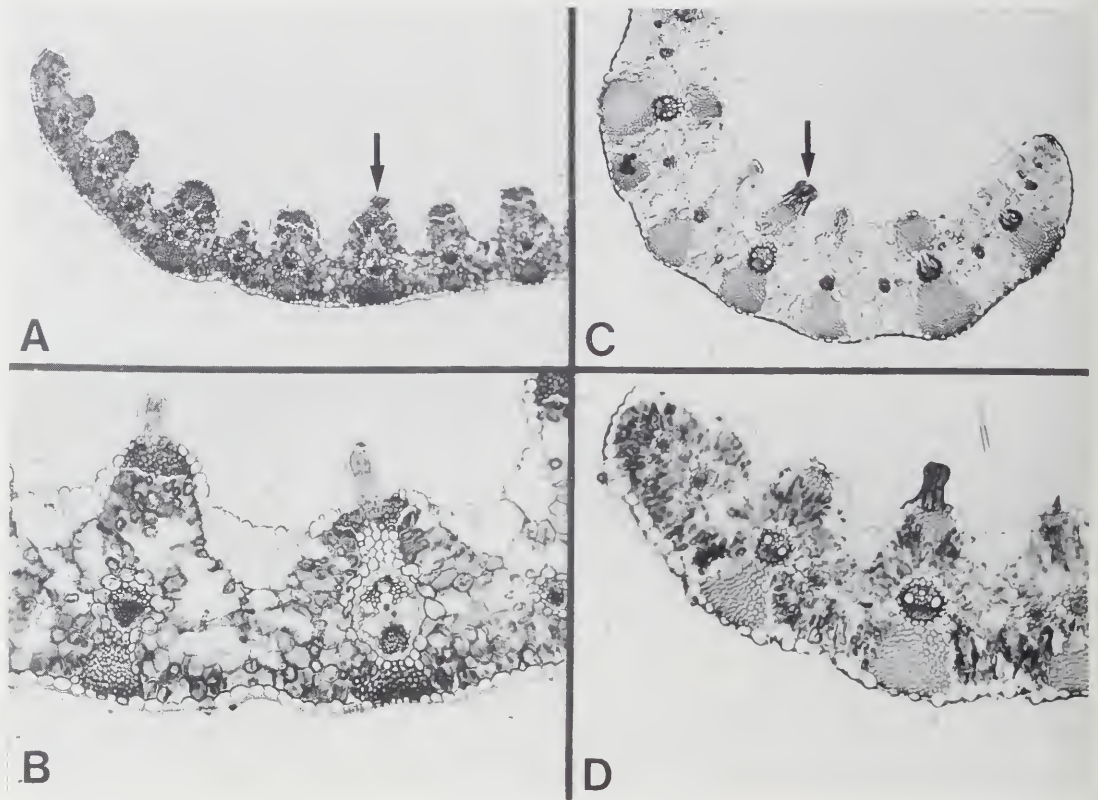
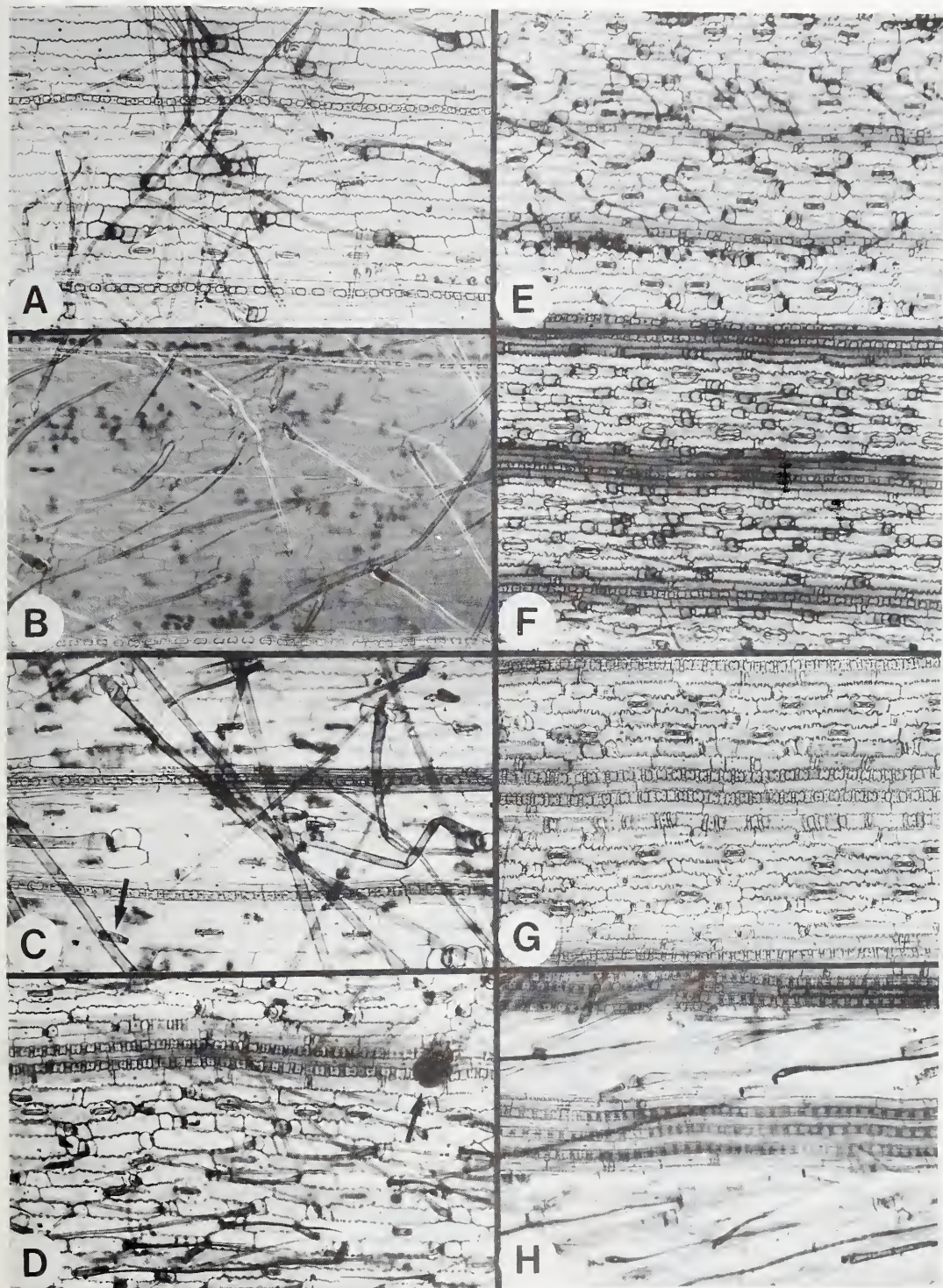
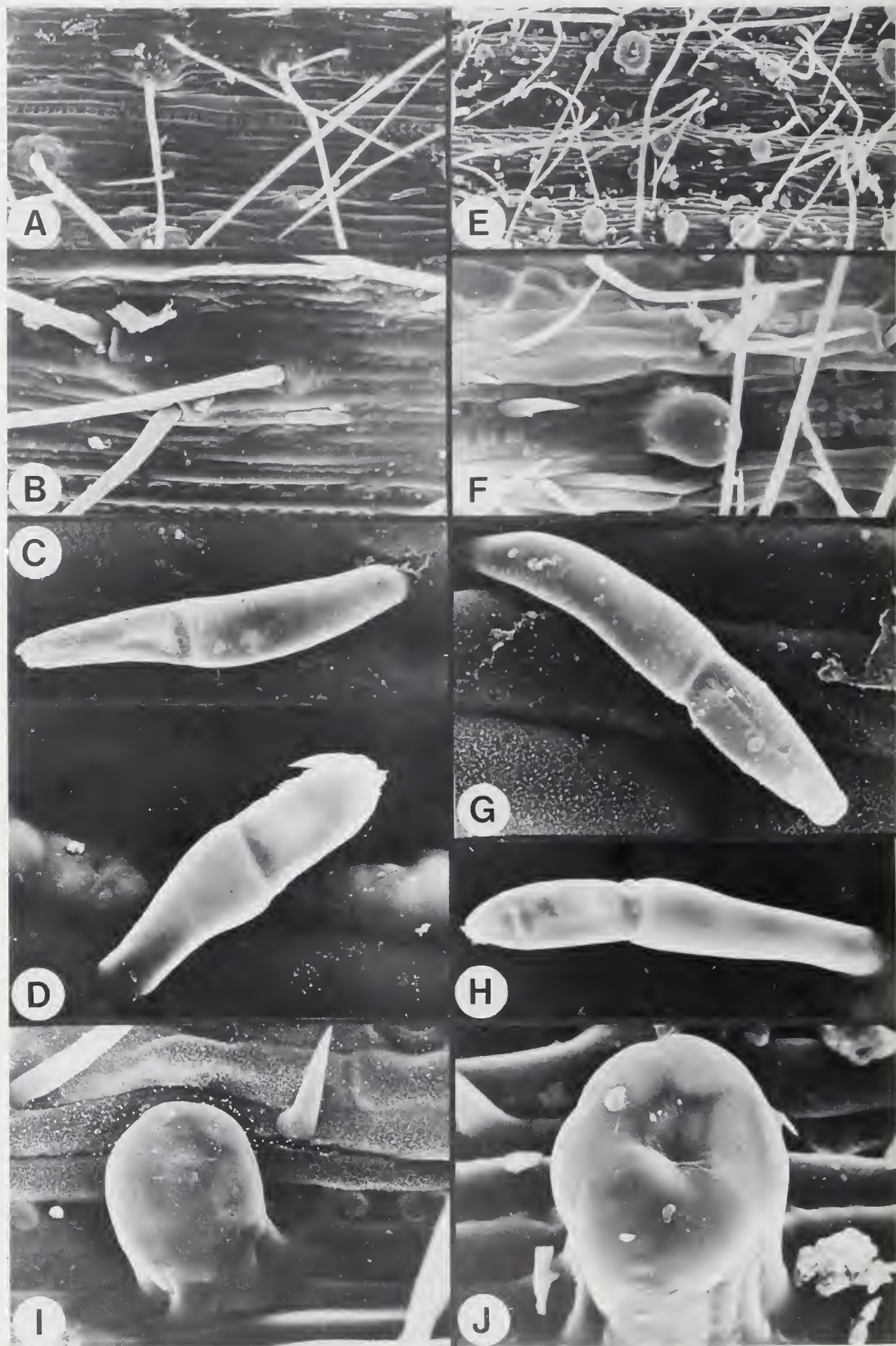


FIGURE 10.2.—*Pentaschistis tomentella*: cross-sectional leaf anatomy of specimens with adaxial leaf glands. A, expanded, broad leaf with medium adaxial ribs and furrows; note gland located adaxially on rib (arrowed). B, detail of dome-shaped adaxial glands; note diffuse type mesophyll. C, inrolled, narrow leaf blade with large amounts of strengthening tissue; note adaxial macrohairs and glands (arrowed). D, detail of adaxial gland, large abaxial sclerenchyma girders and diffuse mesophyll. A, B, *Ellis 5393*; C, *Ellis 5772*; D, *Ellis 5771*. A, $\times 100$; C, $\times 160$; B, D, $\times 250$.

FIGURE 10.3.—*Pentaschistis tomentella*: abaxial epidermis in surface view. A–D, epidermides of soft, flaccid leaves. E–H, epidermides from thicker, tougher, narrower leaf blades. A, typical epidermis of the soft, expanded leaf type with long, flexible macrohairs arising from a base inserted between two inflated epidermal cells; very narrow costal zones are typical (1–3 files wide) and the intercostal zones are wide with elongated long cells. B, interference contrast of soft leaf type showing long, flexible macrohairs. C, macrohairs showing 2–3 inflated epidermal cells associated with the hair base; note microhairs (arrowed). D, costal dome-shaped gland (arrowed), wider costal zone, shorter macrohairs (but with bases inserted between inflated epidermal cells) of a specimen intermediate between the soft leaf type and the tougher inrolled type. E, epidermis of narrow, inrolled leaf type with shorter, narrower intercostal long cells; the macrohairs are also much shorter but structurally identical. F, costal zones wider and intercostal zones narrower; macrohairs associated with inflated epidermal cell. G, wide costal zones with irregularly dumbbell-shaped silica bodies; macrohairs, although very numerous, are not easily visible but the inflated basal cells are evident. H, detail of costal zones and silica bodies and macrohairs; note that the bases may be constricted where they are inserted between the two inflated epidermal cells. A, *Ellis 2198*; B, *Ellis 2199*; C, *Ellis 5392*; D, *Ellis 5393*; E, *Ellis 1141*; F, *Ellis 2458*; G, *Ellis 5772*; H, *Ellis 5771*. All $\times 250$.





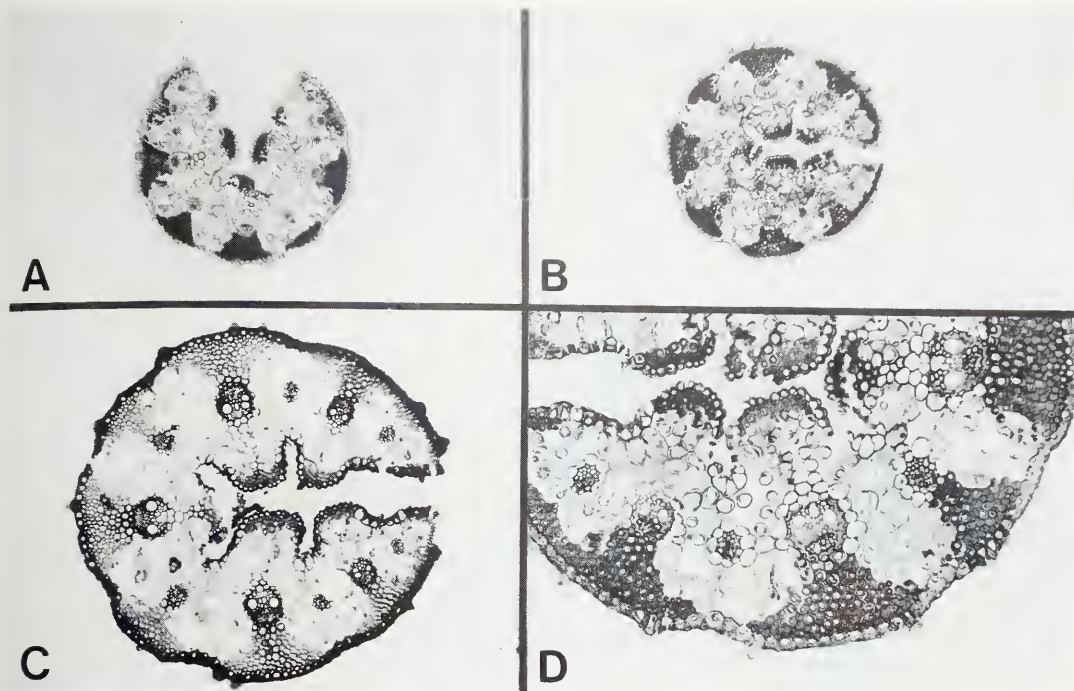


FIGURE 11.1.—*Pentaschistis lima*: transectional leaf anatomy.

A, narrow setaceous leaf outline.

B, permanently infolded leaf blade with well-developed abaxial sclerenchyma girders.

C, more detail of girders, thickened cuticle and abaxial epidermal cells; note bundle sheath extensions on adaxial side of first order vascular bundles.

D, detail of lignified sclerenchyma tissue, very thick-walled abaxial epidermal cells with numerous prickles in section; note the very diffuse nature of the chlorenchyma tissue with large intercellular air spaces, the chlorenchyma cells being larger than the outer bundle sheath cells.

A, Ellis 5995; B, C, D, Ellis 5996. A, B, $\times 100$; C, $\times 160$; D, $\times 250$.

FIGURE 10.4.—*Pentaschistis tomentella*: epidermal ultrastructure. A–D, abaxial epidermis. E–H, adaxial epidermis. I, J, dome-shaped adaxial glands.

A, soft type of leaf with long macrohairs embedded in small raised cushion.

B, stiffer macrohairs without raised cushions.

C, microhair with distal cell slightly tapering and somewhat shorter than the basal cell.

D, microhair with inflated distal cell; basal and distal cells of equal length.

E, adaxial surface with flexible macrohairs and numerous glands located on the adaxial ribs.

F, rib with gland, macrohairs and inflated long cells.

G, adaxial microhair with distal cell slightly shorter than the basal cell.

H, microhair with basal cell much longer than the distal cell.

I, detail of dome-shaped adaxial gland; note that cell outlines are not evident.

J, adaxial gland showing stalk and collar cells surrounding only a few gland cells.

A, C, G, Ellis 5392; B, E, J, Ellis 5771; D, H, Ellis 5772; F, I, Ellis 5080. A, E, $\times 60$; B, F, $\times 200$; I, $\times 450$;

J, $\times 650$; C, $\times 800$; G, H, $\times 950$; D, $\times 1200$.

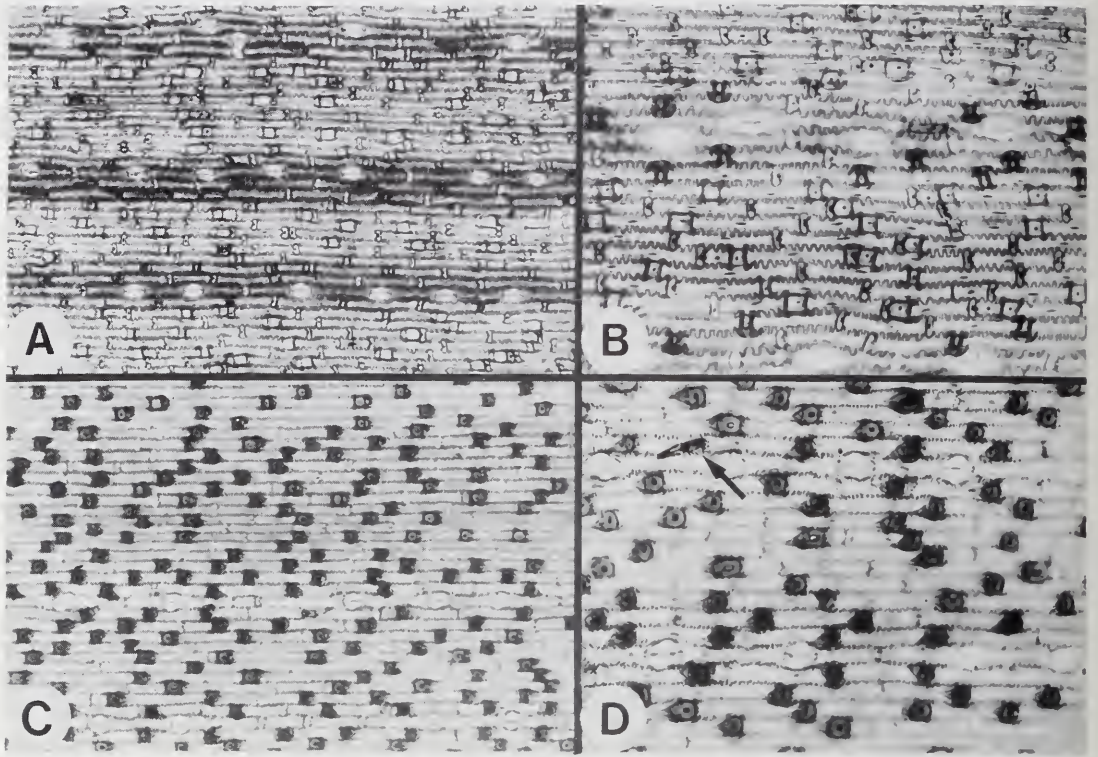


FIGURE 11.2.—*Pentaschistis lima*: abaxial epidermal structure.

A, zonation evident with narrow intercostal zones with stomata and wide costal zones on which costal hooks are common.
 B, detail of single file of low dome-shaped stomata in narrow intercostal zones; note very sinuous, thick-walled intercostal long cells; microhairs present but not visible in photograph; costal zones with tall and narrow silica bodies and numerous hooks visible; note all epidermal cells are nucleate.
 C, specimen in which epidermal zonation not well differentiated; note numerous hooks throughout epidermis and few, irregular stomatal files.

D, detail of hooks, single microhair (arrowed) and stomata.

A, Ellis 5996; B, Ellis 5995; C, D, Ellis 5998. A, C, $\times 160$; B, D, $\times 250$.

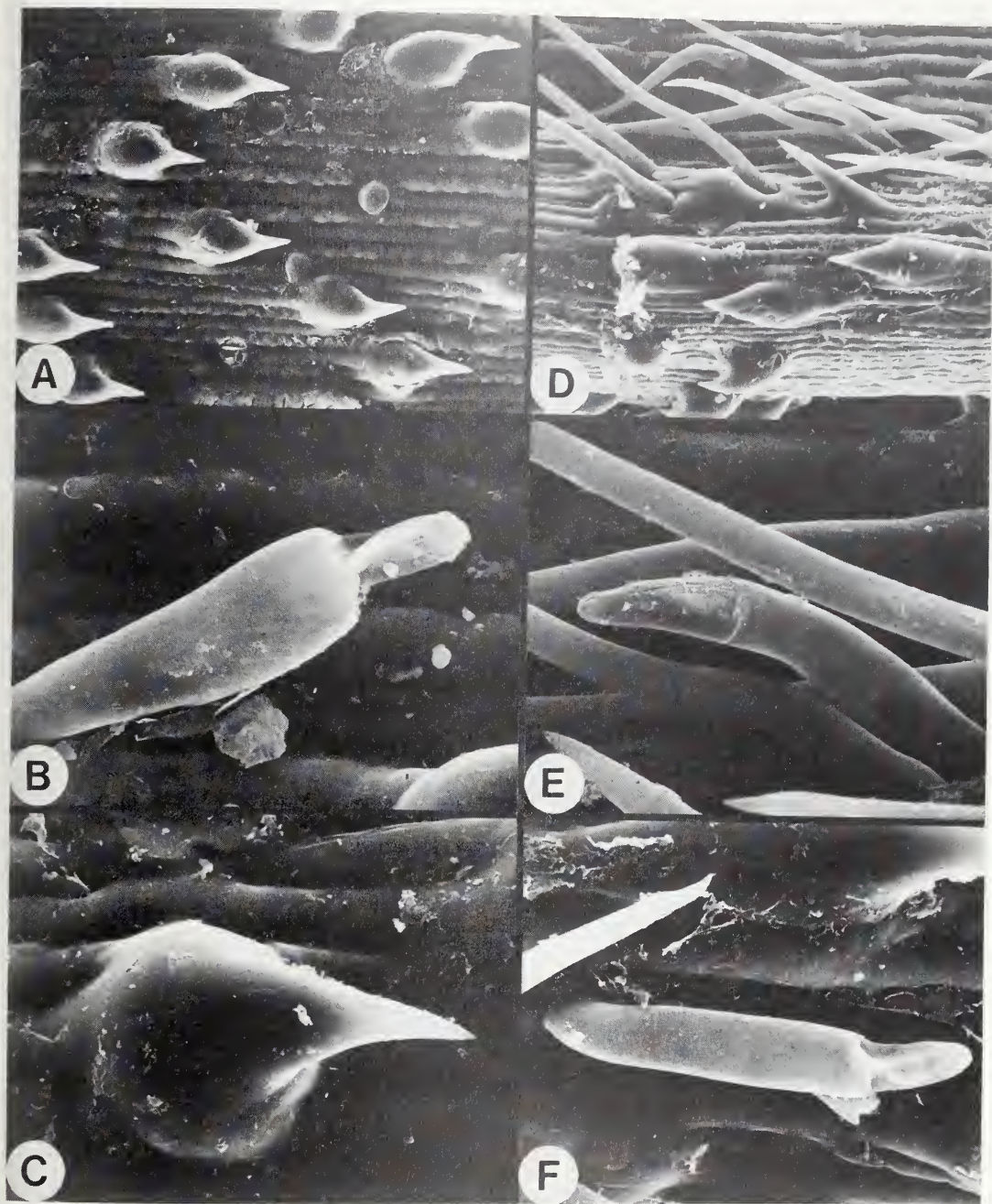


FIGURE 11.3.—*Pentaschistis lima*: epidermal ultrastructure. A–C, abaxial surface. D–F, adaxial surface. A, costal and intercostal hooks all pointing distally and round silica body. B, abaxial microhair with short distal cell. C, detail of hook with sharp, short barb. D, adaxial rib with costal prickles and macrohairs and microhairs on the sides of the furrows. E, finger-like microhair with short distal cell located amongst macrohairs. F, adaxial microhair with short, blunt distal cell. A, F, *Ellis* 5998; B, C, D, E, *Ellis* 5996. A, D, $\times 200$; F, $\times 670$; C, E, $\times 800$; B, $\times 850$.

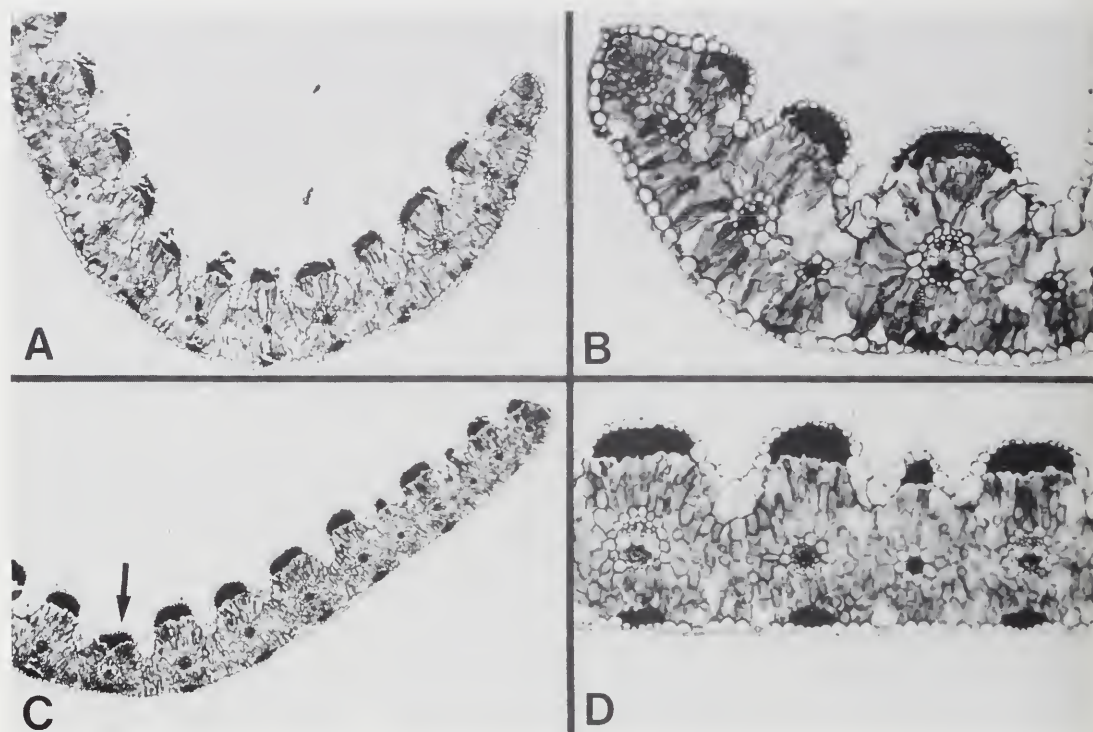


FIGURE 12a.1.—*Pentaschistis patula* form A 'patula': leaf in transverse section.

A, broad leaf blade, slightly inrolled.

B, detail of lateral part of blade showing radial nature of chlorenchyma cell arrangement.

C, broadly folded blade with median vascular bundle (arrowed) structurally identical to lateral first order bundles.

D, detail of specialized chlorenchyma and prominent adaxial sclerenchyma strands.

A, B, *Ellis 5418*; C, D, *Ellis 5781*. A, C, $\times 100$; B, D, $\times 250$.

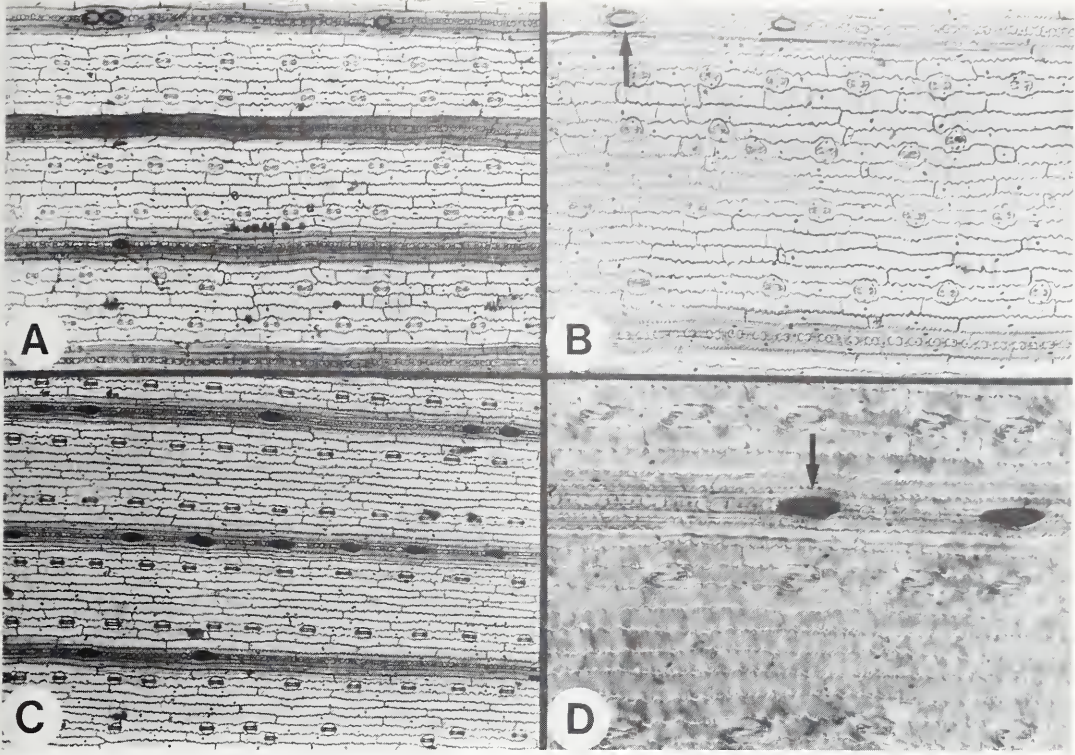


FIGURE 12a.2.—*Pentaschistis patula* form A 'patula': abaxial epidermis.

A, epidermal zonation with costal and intercostal zones clearly distinct.

B, detail of intercostal long cells, stomata and silica bodies; note absence of epidermal appendages except costal prickles (arrowed) with short barbs.

C, epidermal pattern.

D, interference contrast of sinuous long cells, domed stomata and costal prickles (arrowed).

A, B, *Ellis 5781*; C, D, *Ellis 5418*. A, C, $\times 160$; B, D, $\times 250$.

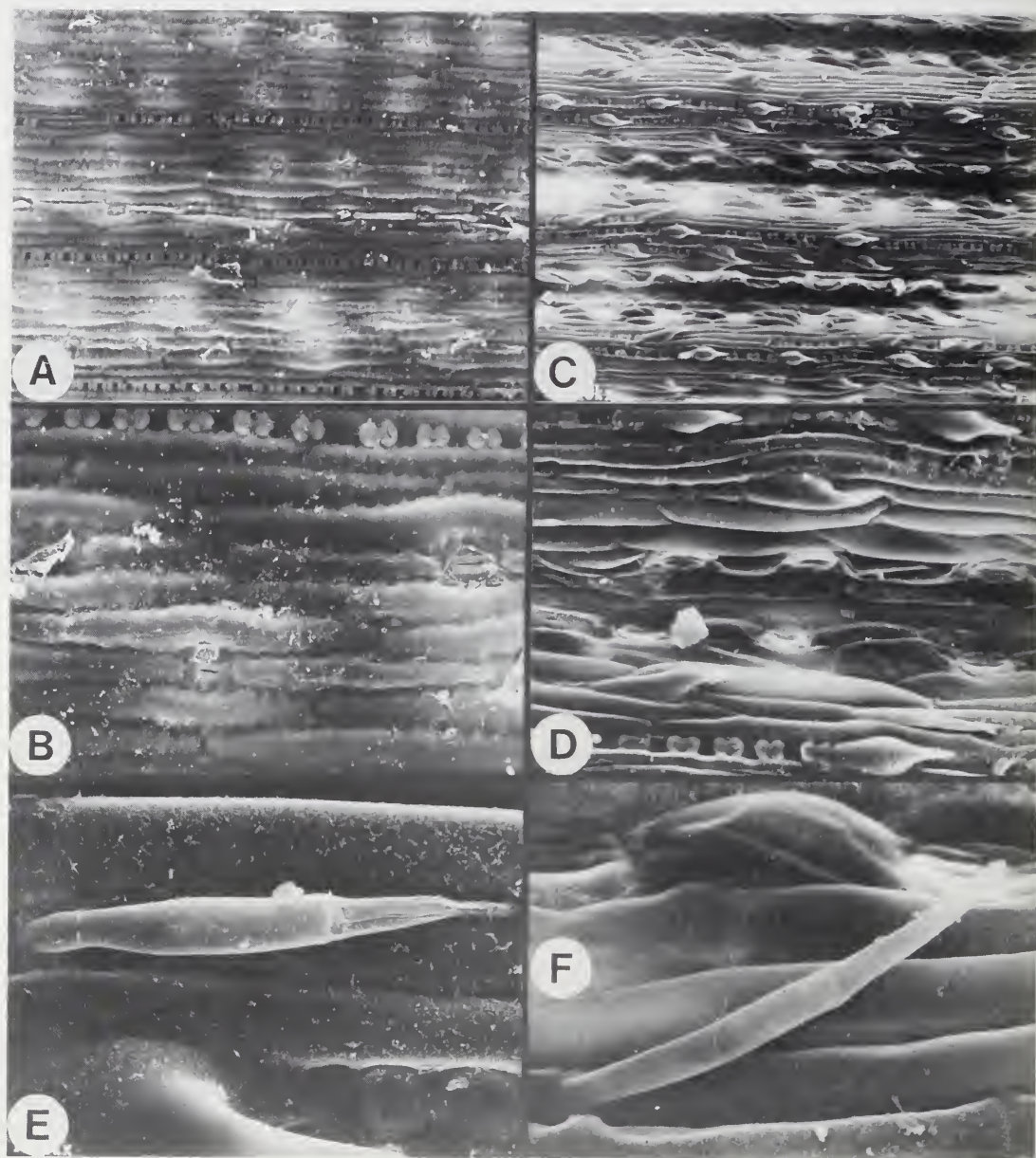


FIGURE 12a.3.—*Pentaschistis patula* form A 'patula': SEM of upper and lower leaf surfaces. A, B, abaxial epidermis. C, D, adaxial epidermis.

A, costal and intercostal zones and no epidermal appendages, including microhairs.

B, intercostal long cells inflated, with a slightly fusiform shape and silica bodies dumbbell-shaped.

C, adaxial surface with ribs and furrows.

D, prickles and silica bodies on costal ribs and stomata in furrows. E, finger-like adaxial microhair with tapering distal cell.

F, rare, very thin adaxial microhair.

A–F, *Ellis 5418*. A, C, $\times 60$; B, D, $\times 200$; F, $\times 600$; E, $\times 850$.

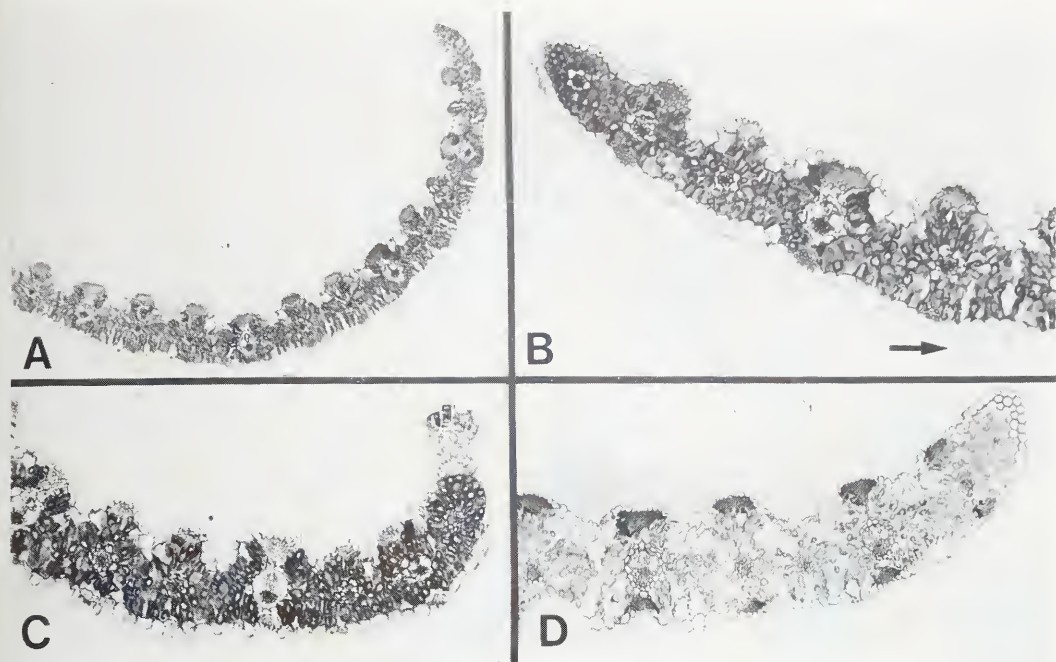


FIGURE 12c.1.—*Pentaschistis patula* form C 'heteroplo': leaf blade in transverse section.

A, slightly inrolled but, nevertheless expanded outline.

B, typical mesic type anatomy; note absence of continuous cuticle and raised cushion bases of macrohairs (arrowed).

C, interference contrast showing marginal stalked gland.

D, detail of anatomical structure with diffuse mesophyll, sclerenchyma strands and continuous but thin abaxial cuticle.

A, B, *Ellis* 2438; C, *Ellis* 2443; D, *Ellis* 5412. A, $\times 100$; B–D, $\times 250$.

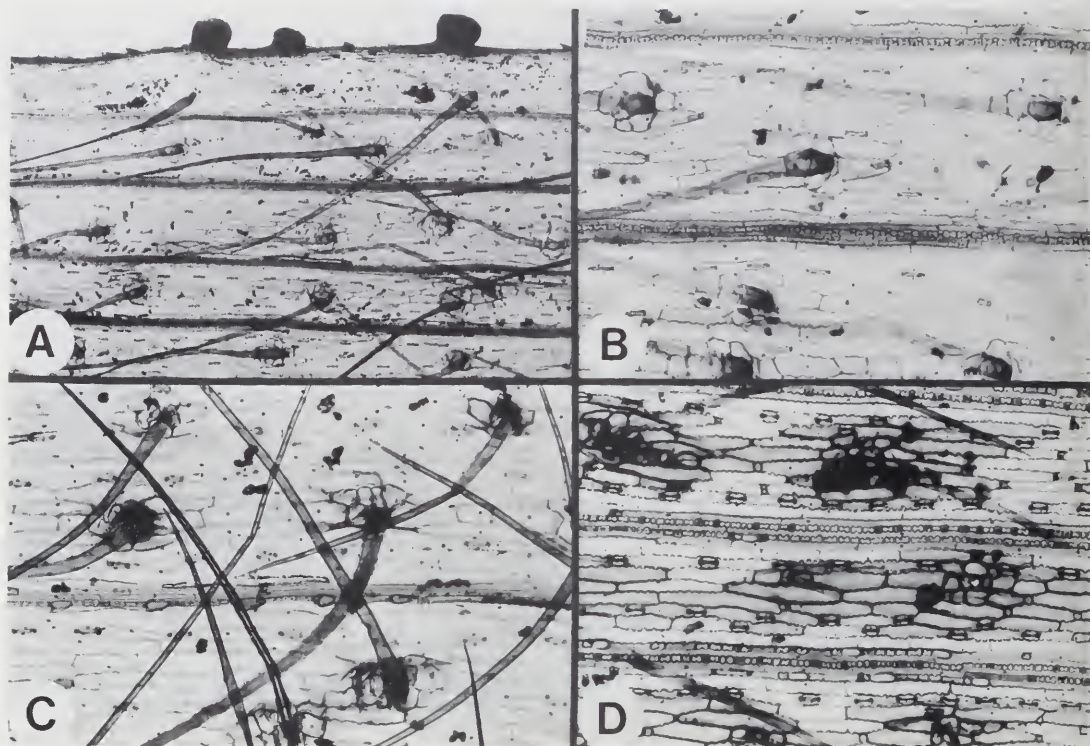


FIGURE 12c.2.—*Pentaschistis patula* form C 'heteroplo': abaxial epidermis.

A, lateral part of lamina with marginal glands; note numerous macrohairs.

B, detail of stiff macrohairs with thickened walls and constricted bases inserted between numerous modified epidermal cells; note elongated rectangular long cells with slightly wavy walls, dumbbell silica bodies and microhairs.

C, detail of macrohairs and their cushion bases.

D, differential staining of modified epidermal cells associated with macrohair bases evident; note that intercostal long cells are hexagonal in outline as is sometimes the case in *P. pallida* form B as well (Figure 7b.2F).

A, B, *Ellis* 5412; C, *Ellis* 5424; D, *Ellis* 2438. A, $\times 100$; B–D, $\times 250$.

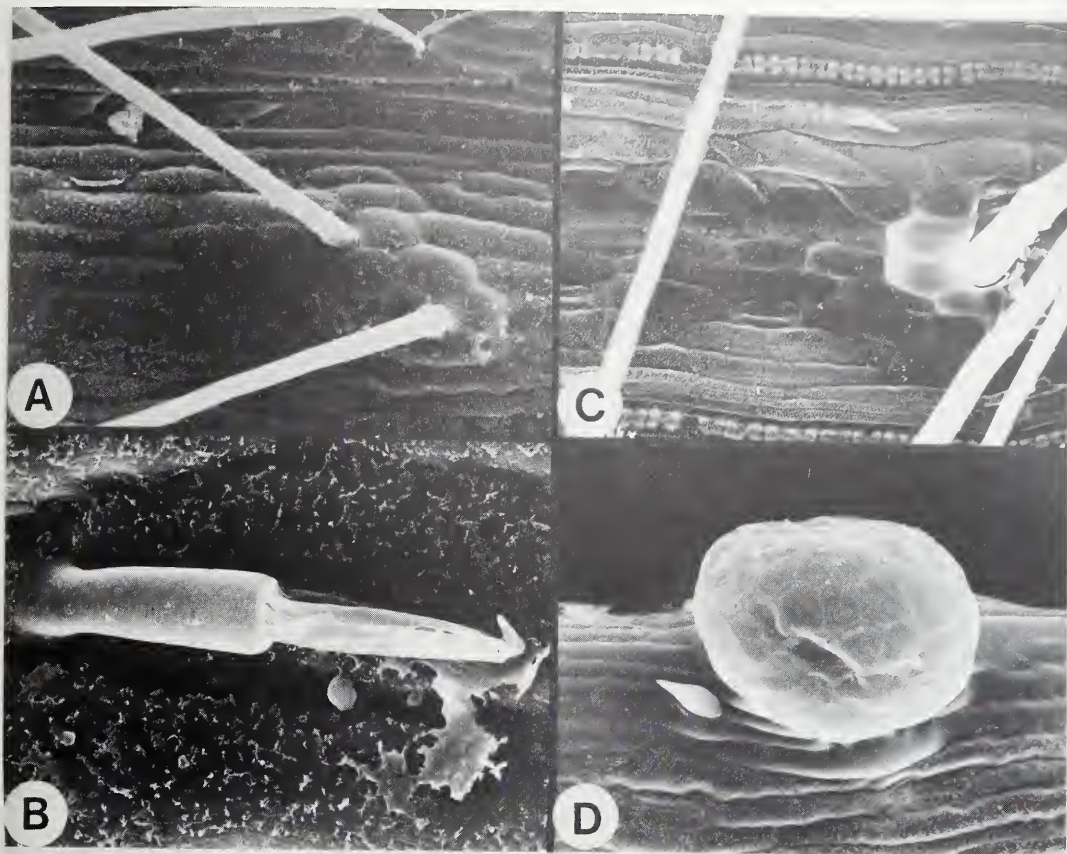


FIGURE 12c.3.—*Pentaschistis patula* form C 'heteroplo': leaf blade surface ultrastructure. A, B, abaxial epidermis. C, D, adaxial epidermis.

A, stiff macrohairs arising from raised cushion bases.

B, microhair with tapering distal cell and both cells of similar length.

C, macrohairs and cushion bases, costal silica bodies and prickles.

D, marginal gland with very short stalk; convex surface with angular glandular cells.

A, *Ellis 5424*; B–D, *Ellis 5412*. A, C, $\times 200$; D, $\times 250$; B, $\times 1000$.

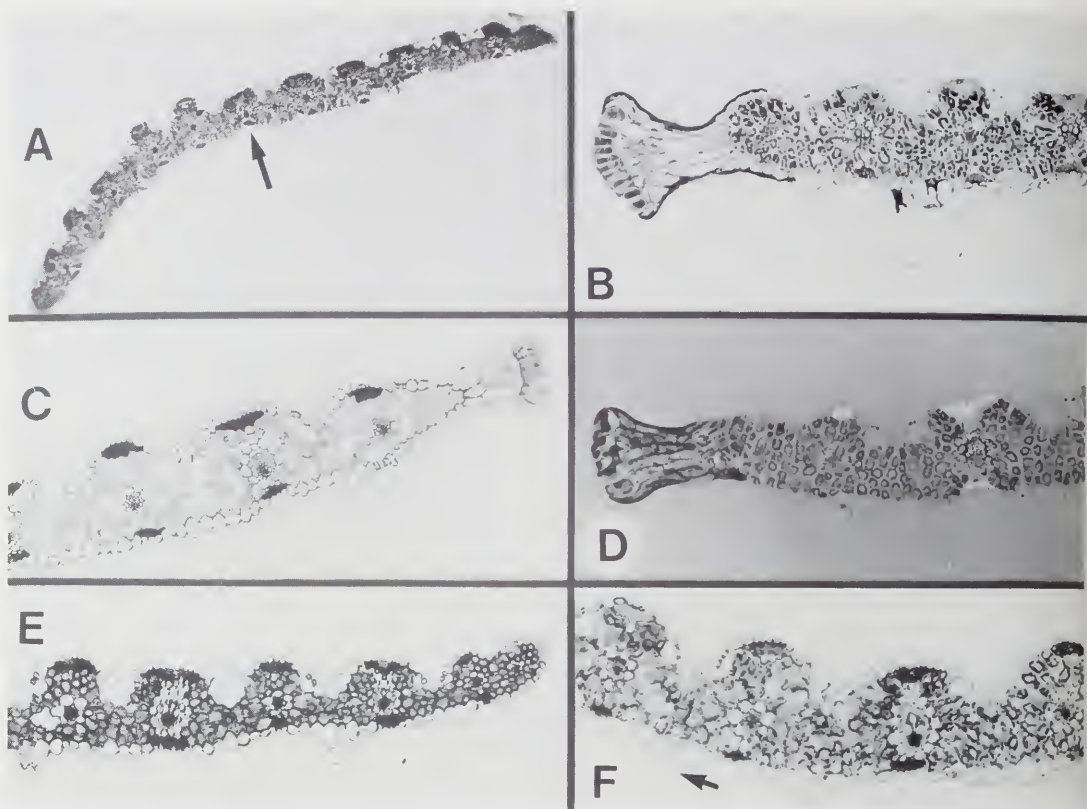
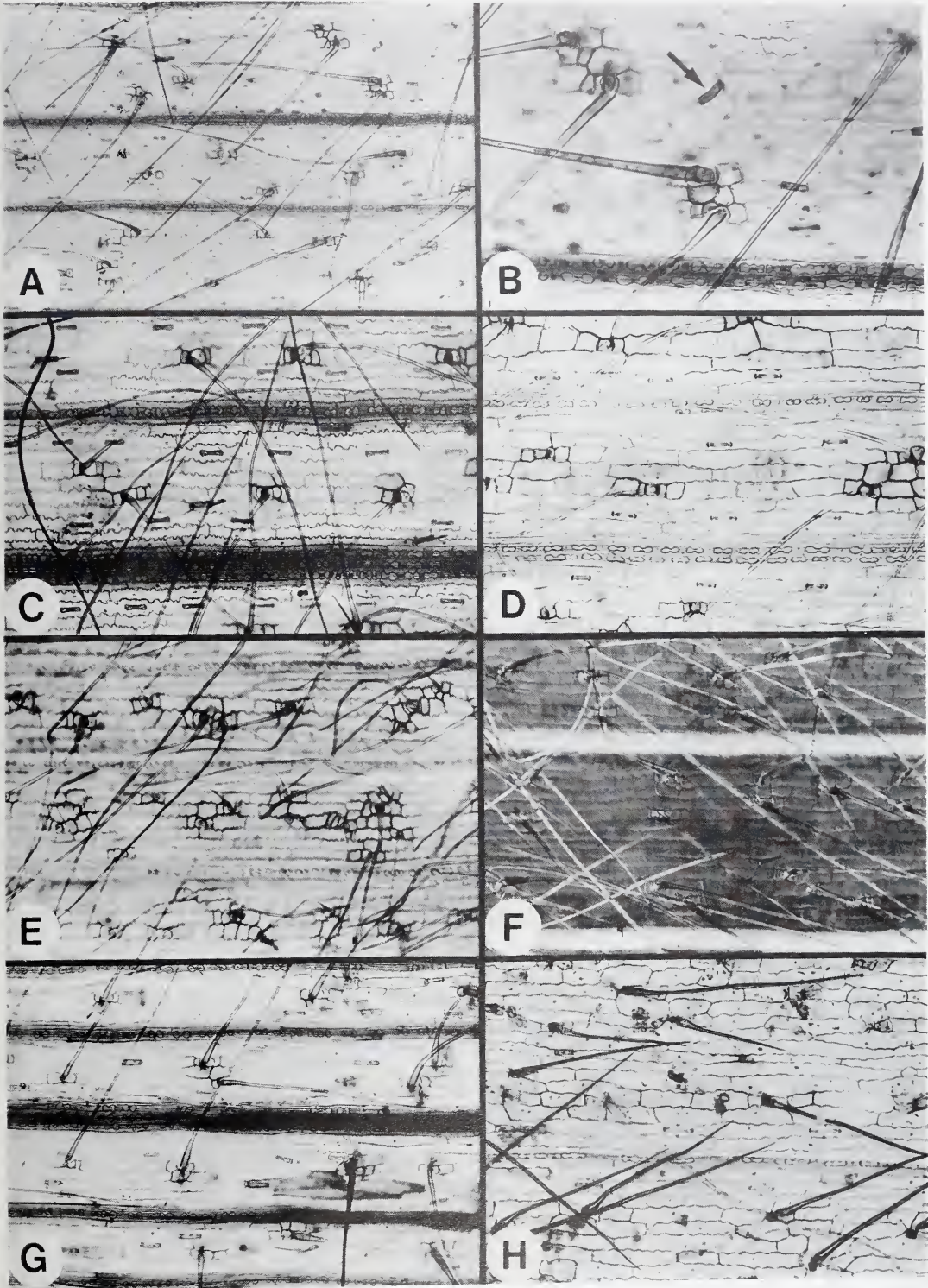


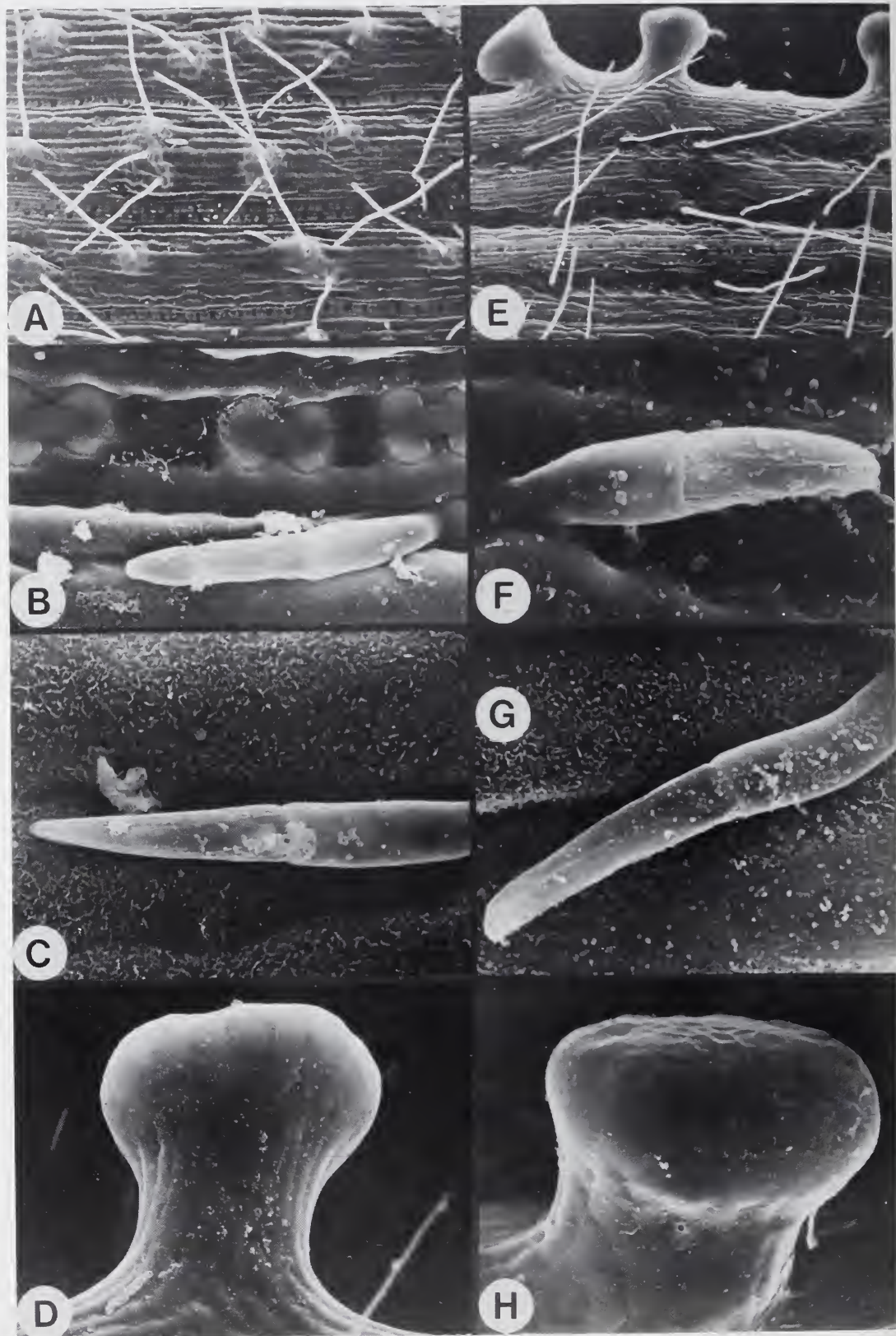
FIGURE 13a.1.—*Pentaschistis airoides* subsp. *airoides*: transsectional leaf anatomy.

- A, expanded leaf outline with median vascular bundle (arrowed) structurally identical to lateral first order bundles.
 B, detail of leaf margin showing marginal gland in section; note elongated stalk cells and collar cells covered by thick cuticle.
 C, long-stalked marginal gland with small sclerenchyma strands associated with all vascular bundles.
 D, marginal gland and diffuse mesophyll tissue under interference contrast illumination.
 E, margin in area without gland showing abrupt margin which does not taper relative to the thickness of the leaf blade.
 F, anatomical detail with diffuse mesophyll, thin cuticle and slightly raised basal cells of macrohairs (arrowed).
 A, B, Ellis 5394; C, Ellis 5632; D, Ellis 1702; E, Ellis 5126; F, Ellis 2555. A, $\times 100$; B–F, $\times 250$.

FIGURE 13a.2.—*Pentaschistis airoides* subsp. *airoides*: abaxial epidermis in surface view showing consistent epidermal structure.

- A, epidermal pattern with very narrow costal zones; note frequency of macrohairs.
 B, detail of macrohair bases inserted between a few modified epidermal cells; note silica body shape tending to the nodular type and the microhairs (arrowed).
 C, thin, flexible macrohairs with 2–4 inflated basal epidermal cells.
 D, macrohairs and their bases, intercostal long cells and silica bodies.
 E, differential staining of epidermal cells associated with the macrohair bases.
 F, interference contrast of macrohairs and narrow costal zones.
 G, epidermal pattern and shorter, stiffer macrohairs.
 H, long cell outline, macrohairs and nodular silica bodies.
 A, B, Ellis 5112; C, Ellis 5394; D, Ellis 2555; E, Ellis 636; F, Ellis 1633; G, Ellis 5126; H, Ellis 5121. A, $\times 160$; C–H, $\times 250$; B, $\times 400$.





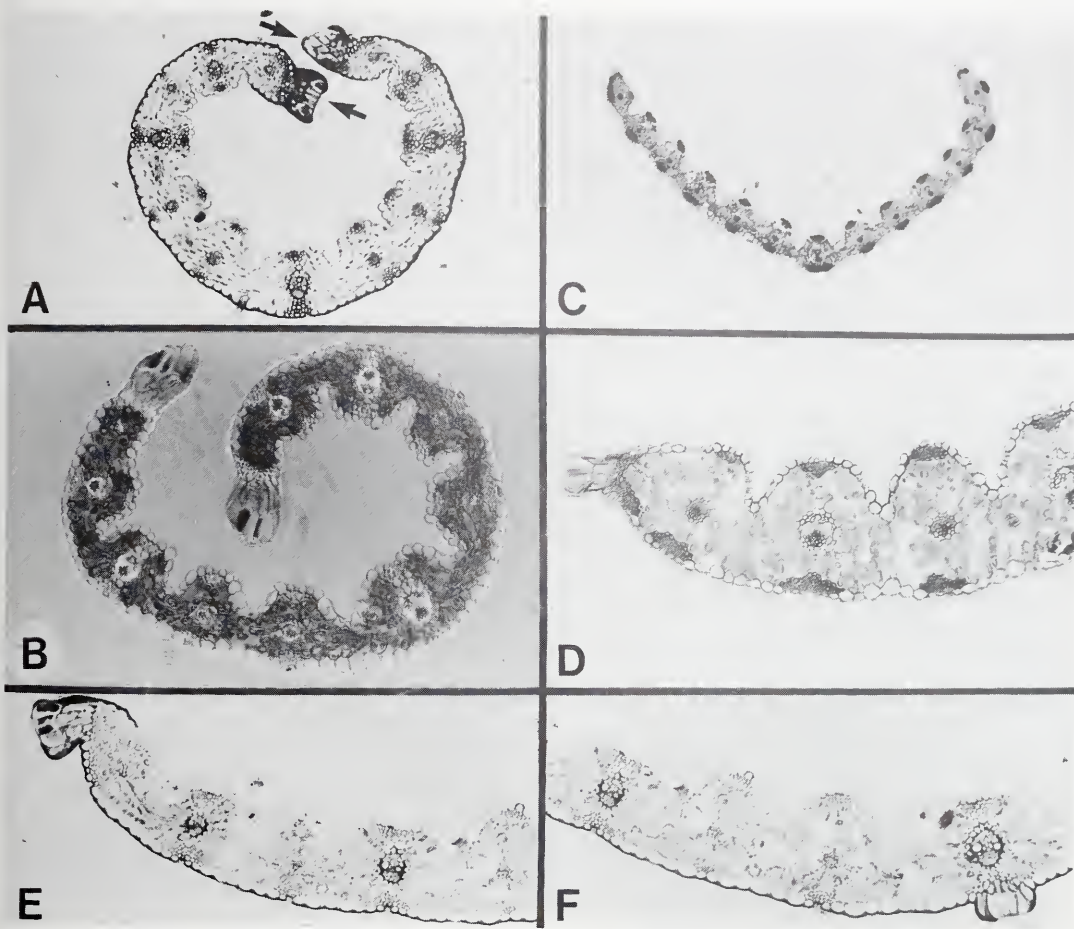


FIGURE 13b.1.—*Pentaschistis airoides* subsp. *jugorum*: leaf blade in transverse section.

A, inrolled leaf outline; note glands on both margins (arrowed).

B, inrolled blade with glands on both margins; interference contrast.

C, more open outline with no glands visible on margins in the area sectioned.

D, margin with stalked gland; note sclerenchyma strands and diffuse mesophyll.

E, margin with stalked gland.

F, raised, but unstalked, gland located abaxially over the midrib.

A, *Ellis* 2366; B, *Ellis* 2376; C, *Ellis* 5680; D, *Ellis* 5695; E, F, *Ellis* 2364. A, C, $\times 100$; B, D–F, $\times 250$.

FIGURE 13a.3.—*Pentaschistis airoides* subsp. *airoides*: epidermal ultrastructure. A–D, abaxial surface. E–H, adaxial surface.

A, intercostally located macrohairs on slightly raised bases.

B, tricellular microhair and dumbbell silica bodies.

C, normal microhair with tapering distal cell; basal and distal cells of equal length.

D, marginal gland showing elongated stalk.

E, adaxial surface with marginal glands, adaxial ribs and thin macrohairs.

F, thicker and shorter adaxial microhair; the distal cell does not taper to a point.

G, longer, more slender adaxial microhair.

H, multicellular gland on leaf margin.

A, B, D, E, F, *Ellis* 5394; C, G, H, *Ellis* 5632. A, E, $\times 70$; D, $\times 250$; H, $\times 330$; B, $\times 800$; C, $\times 1100$; F, G, $\times 1500$.

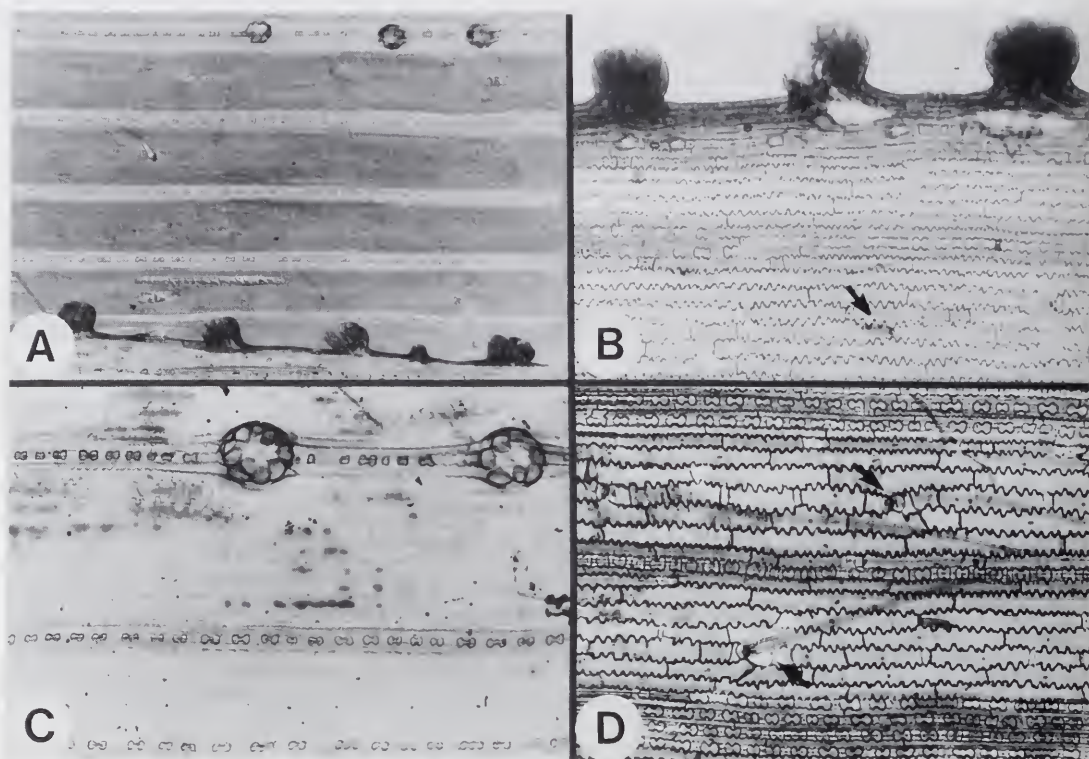


FIGURE 13b.2.—*Pentaschistis airoides* subsp. *jugorum*: abaxial epidermal structure.

A, costal and intercostal zones; note marginal glands at bottom of photograph and midrib glands at top.

B, profile of marginal glands with short stalks, moderately sinuous long cells, dumbbell-shaped silica bodies and microhairs (arrowed).

C, detail of unstalked glands situated over the median vascular bundle; silica body shape clearly evident.

D, epidermal detail showing stiff macrohairs with thickened walls and with inflated epidermal cells present where hair is inserted into the blade (arrowed).

A, Ellis 2376; B, D, Ellis 5695; C, Ellis 2364. A, $\times 160$; B–D, $\times 250$.

FIGURE 13b.3.—*Pentaschistis airoides* subsp. *jugorum*: epidermal ultrastructure. A–D, abaxial epidermis. E–H, adaxial epidermis.

A, distribution and frequency of macrohairs.

B, macrohair with inflated basal cells; note dumbbell-shaped silica bodies.

C, abaxial microhair with distal cell not tapering.

D, marginal concave gland.

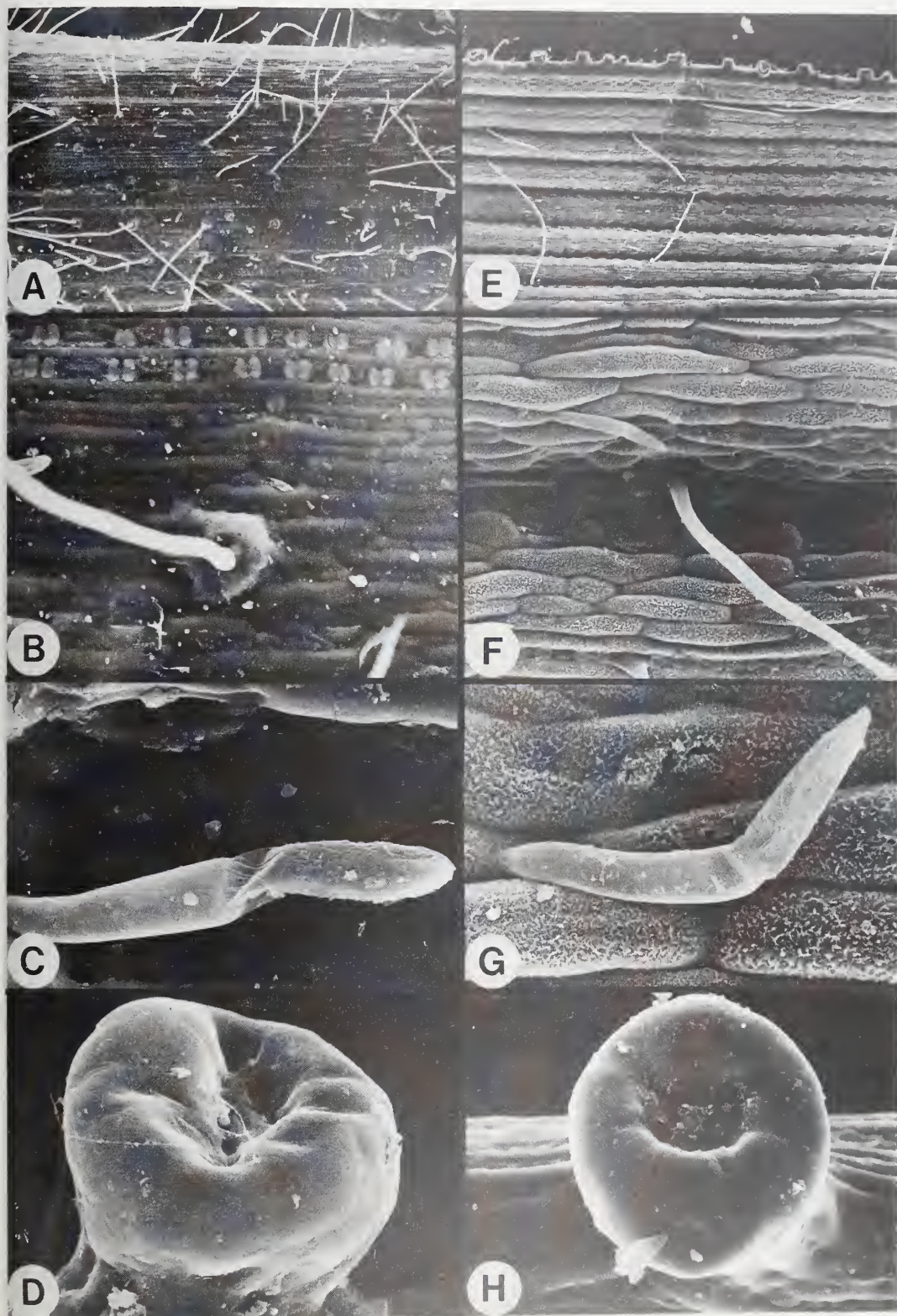
E, adaxial view of blade showing few macrohairs, ribs and marginal glands.

F, adaxial ribs and furrow with macrohair.

G, microhair with tapering distal cell; basal cell somewhat longer than distal cell.

H, concave marginal gland.

A, D, E, F, G, Ellis 5695; B, C, H, Ellis 5680. A, E, $\times 20$; B, F, $\times 200$; H, $\times 380$; D, $\times 450$; C, G, $\times 760$.



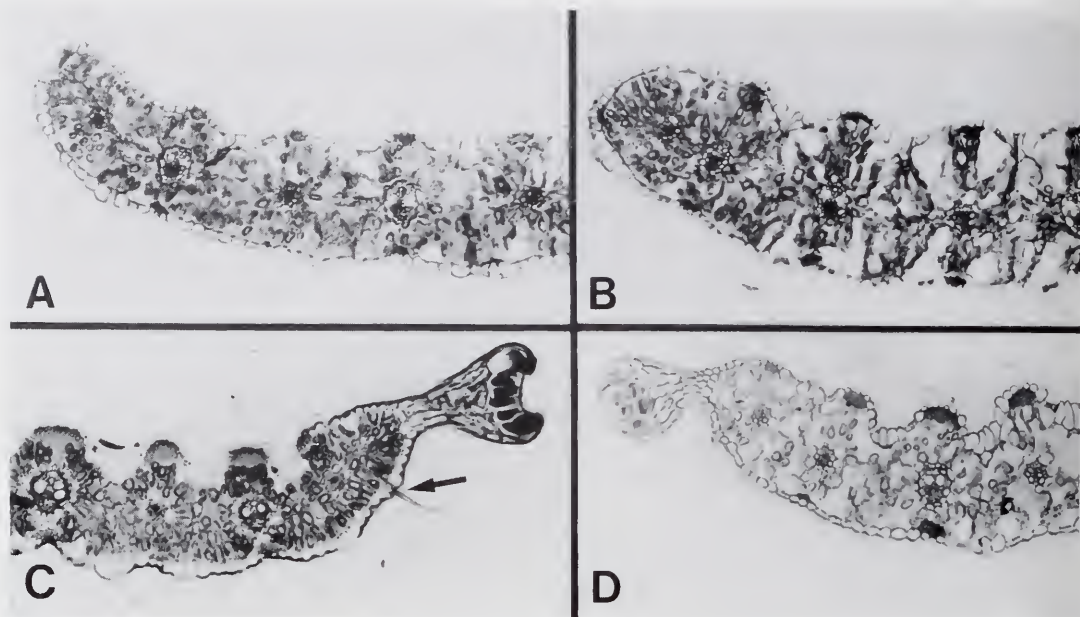


FIGURE 14.1.—*Pentaschistis capillaris*: leaf in transverse section.

A, lateral part of blade with diffuse mesophyll and abrupt margin.

B, abrupt leaf margin, diffuse chlorenchyma, shallow adaxial furrows, small bulliform cells and very small sclerenchyma strands.

C, pedicelled marginal gland with crateriform apex; note bases of sectioned macrohairs (arrowed).

D, club-shaped marginal gland and very diffuse mesophyll.

A, *Ellis 5411*; B, *Ellis 5410*; C, *Ellis 5782*; D, *Spies 3412*. A–D, $\times 250$.

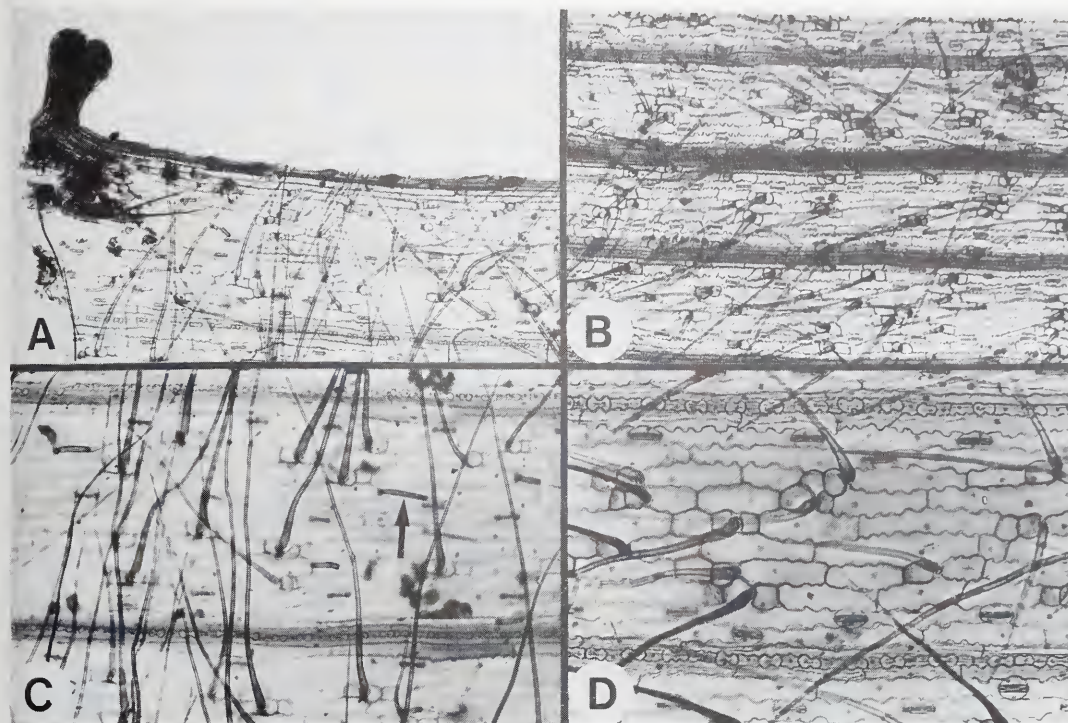


FIGURE 14.2.—*Pentaschistis capillaris*: abaxial epidermis.

A, lateral part of blade with stalked, club-shaped gland and many macrohairs.

B, epidermal pattern with narrow costal zones and numerous macrohairs in the intercostal zones.

C, detail of slender macrohairs inserted between two inflated epidermal cells; note dumbbell-shaped silica bodies and microhairs (arrowed).

D, epidermal cell detail showing modified intercostal cells associated with the insertion of the macrohairs; note stomata, undulating long cell walls and silica bodies.

A, C, *Spies 3412*; B, *Ellis 5782*; D, *Ellis 5411*. A, B, $\times 160$; C, $\times 250$; D, $\times 400$.

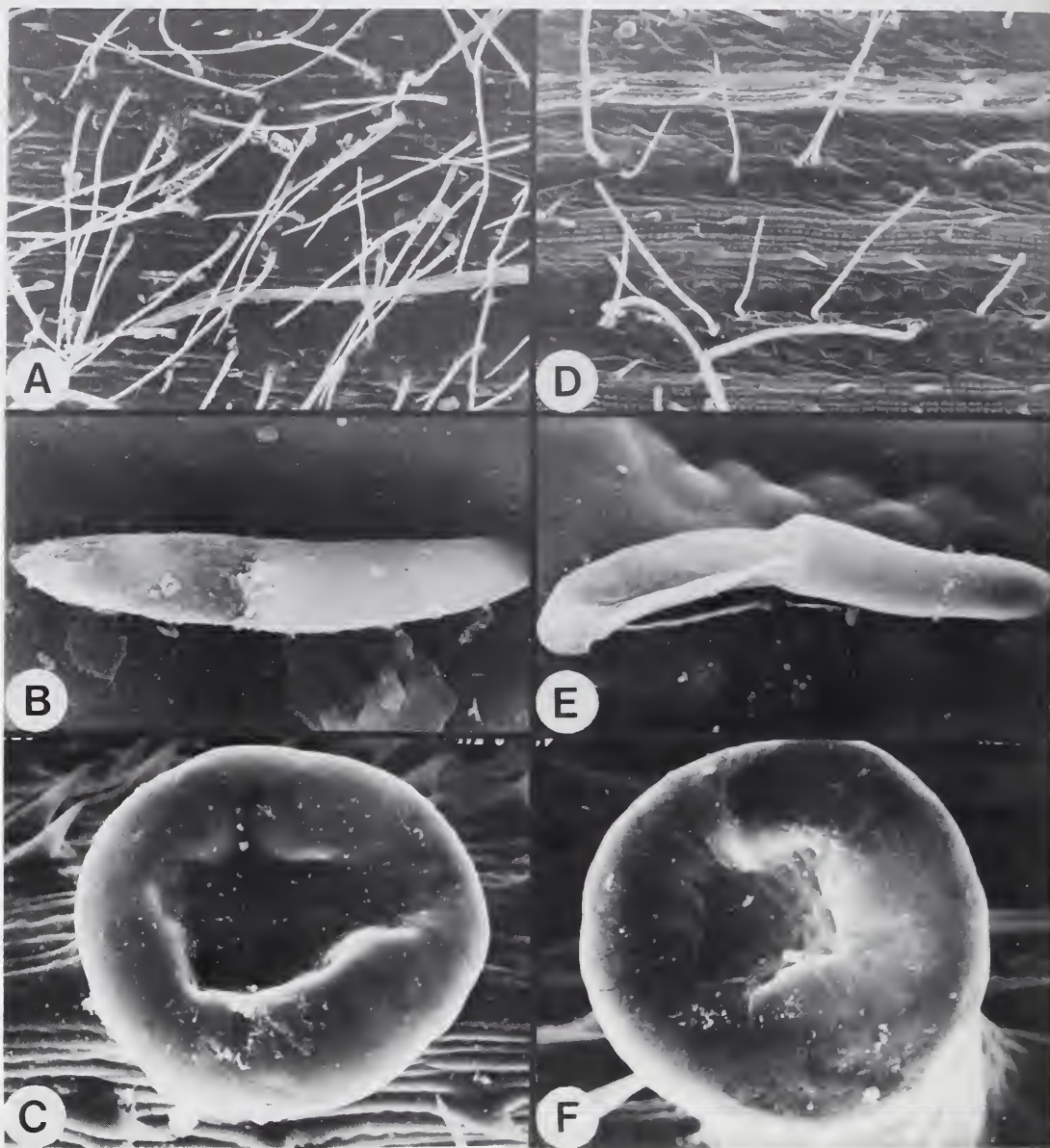


FIGURE 14.3.—*Pentaschistus capillaris*: leaf blade ultrastructure. A–C, abaxial epidermis. D–F, adaxial epidermis.

A, dense pubescence on abaxial surface.

B, microhair with distal cell slightly shorter than basal cell.

C, crateriform, marginal gland.

D, adaxial pubescence not as dense as that on abaxial surface.

E, adaxial microhair with distal cell not tapering.

F, marginal gland showing collar cells surrounding sunken gland cells.

A, D, *Ellis* 5410; B, C, *Spies* 3412; E, F, *Ellis* 5782. A, D, $\times 60$; C, F, $\times 300$; D, $\times 1200$; B, $\times 1300$.

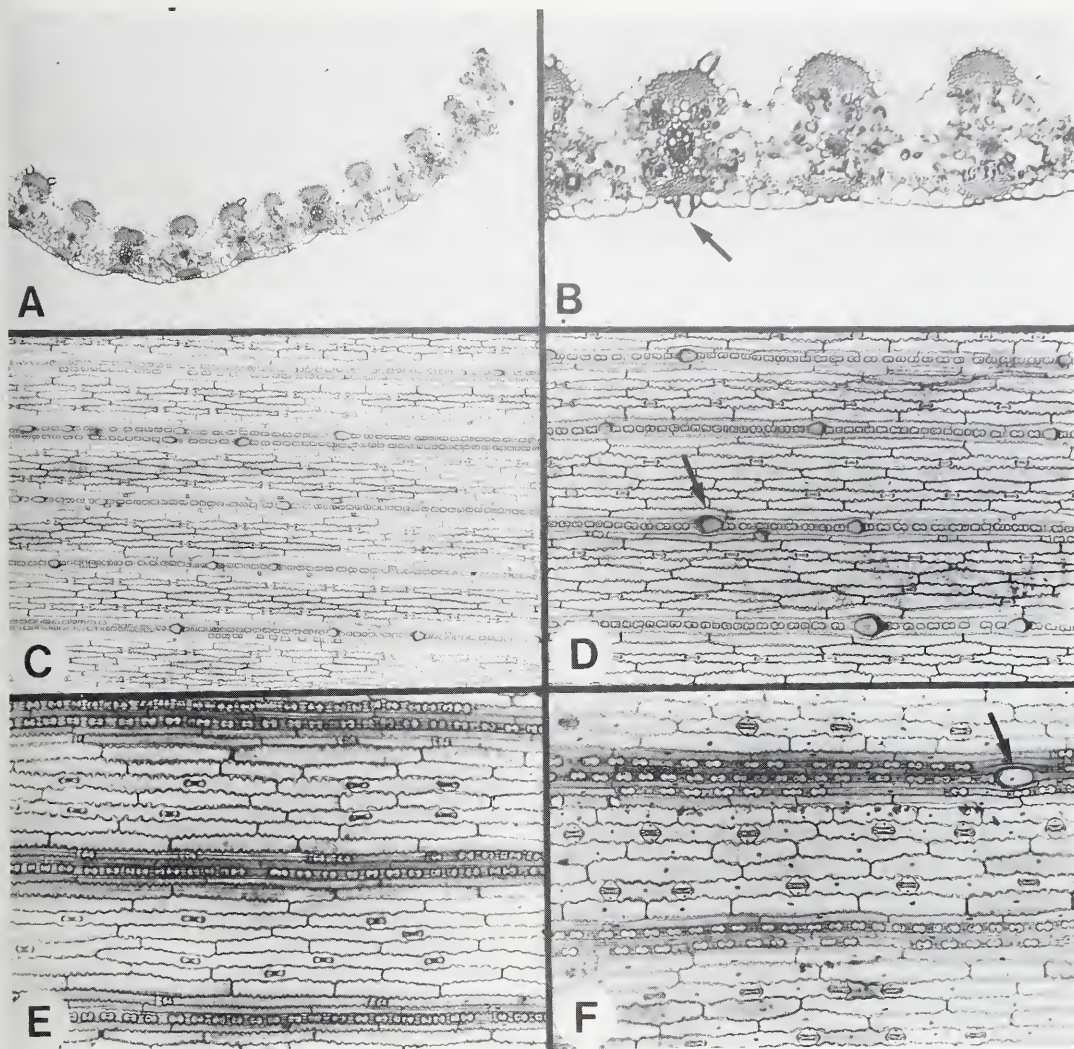


FIGURE 15.1.—*Pentaschistis aristifolia*: leaf blade anatomy. A, B, transverse sections. C–F, abaxial epidermis. A, expanded outline with truncated margin. B, detail of adaxial ribs and furrows, large adaxial sclerenchyma strands and epidermal prickly hairs (arrowed). C, epidermal pattern with distinct costal and intercostal zones. D, detail of fusiform long cells; note prickly hairs (arrowed) and absence of other epidermal appendages. E, epidermal pattern with sinuous long cells, stomata and dumbbell-shaped silica bodies. F, epidermal cell arrangement; note prickly hair (arrowed). A, B, Ellis 5414; C, D, Ellis 2463; E, Ellis 1722; F, Ellis 5414. A, C, $\times 100$; D, $\times 160$; B, E, F, $\times 250$.

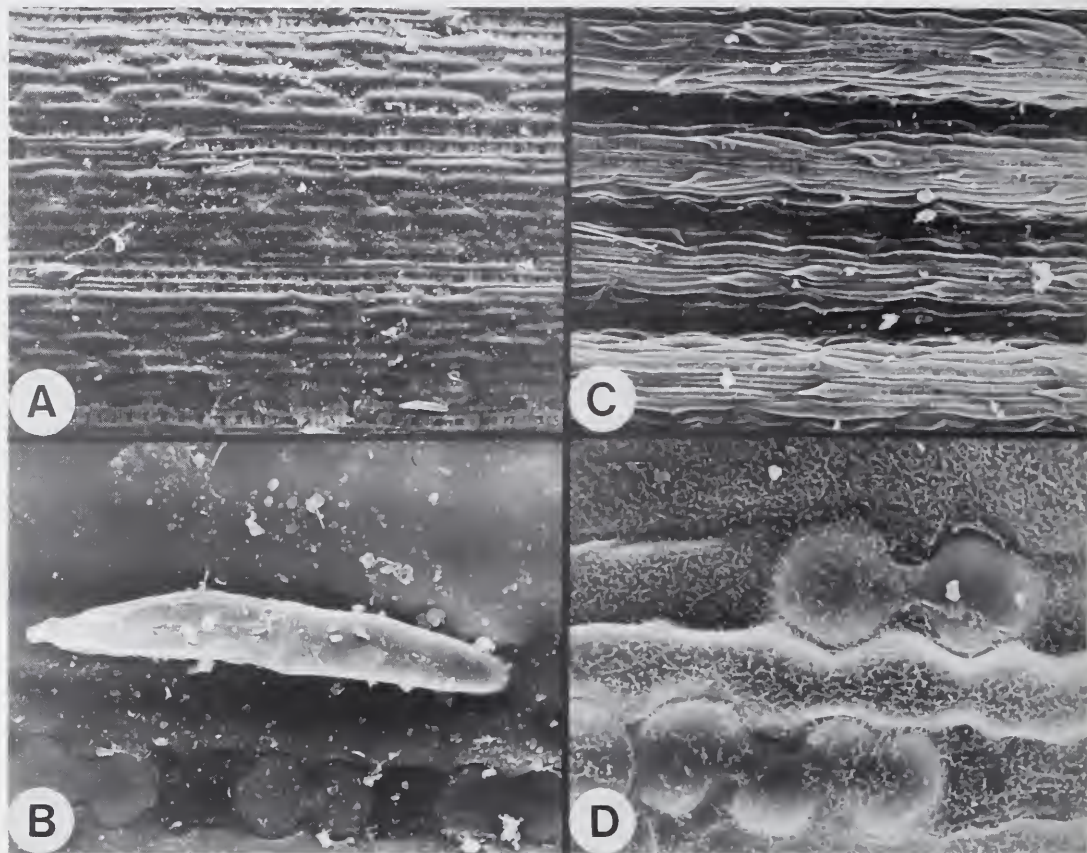


FIGURE 15.2. — *Pentaschistis aristifolia*: epidermal ultrastructure. A, B, abaxial epidermis. C, D, adaxial epidermis. A, featureless epidermis; note few costal prickles. B, rare microhair, finger-like with tapering distal cell. C, ribs and furrows of adaxial surface. D, nodular and dumbbell adaxial silica bodies. A–D, *Ellis 5414*. A, C, $\times 60$; B, $\times 700$; D, $\times 1000$.



FIGURE 16.1. — *Pentaschistis trisetoides*: leaf in transverse section.

A, very thin, expanded leaf blade with mesic mesophyll type, 5 first order bundles in leaf section interspaced with 1 or 2 smaller bundles, no marginal glands or abaxial appendages visible, poor reconstitution hampers further interpretation.

A, *Schimper 904*. A, $\times 100$.

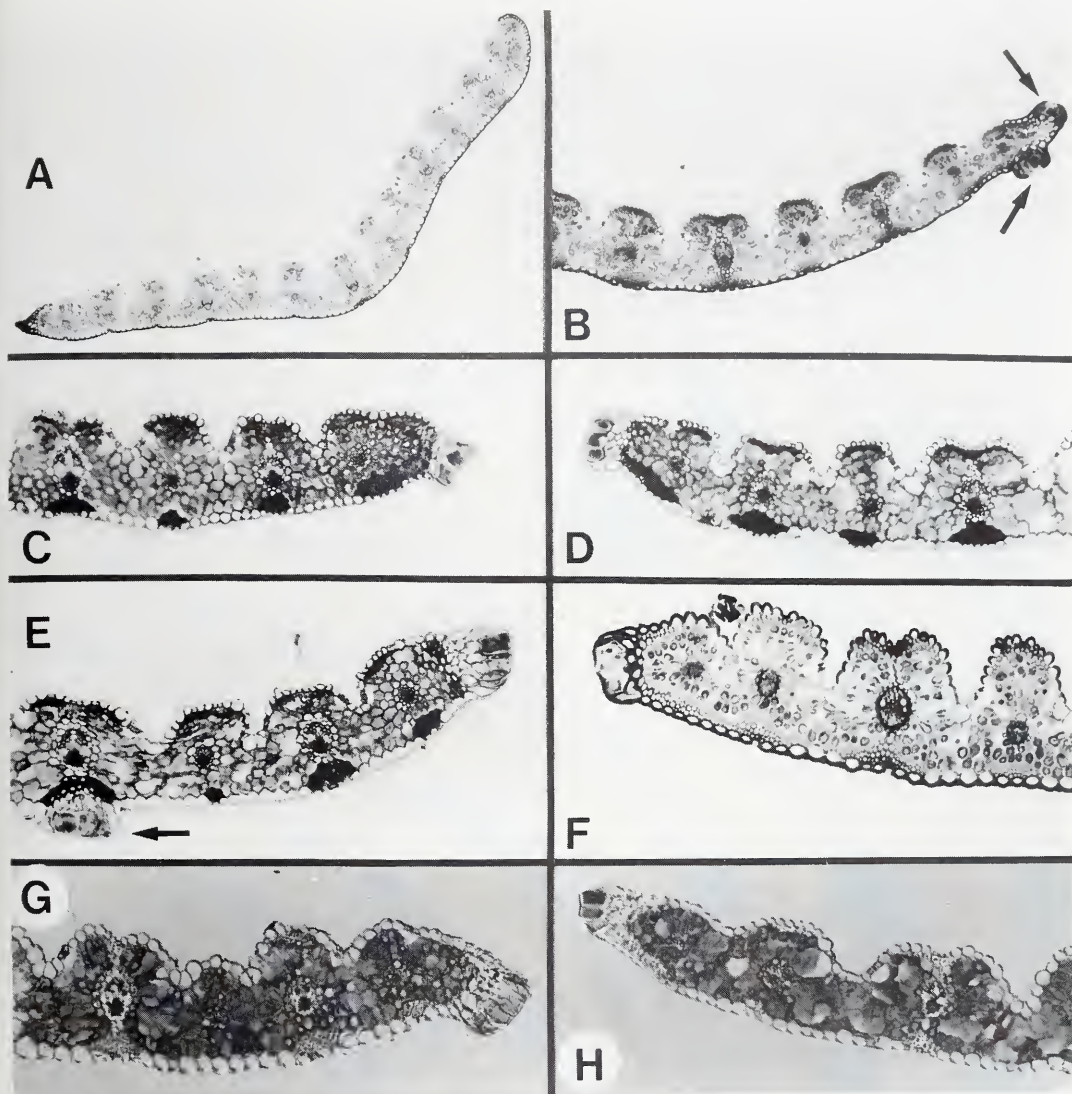


FIGURE 17.1.—*Pentaschistis galpinii*: leaf blade in transection.

A, expanded, slightly infolded outline.

B, lateral part of blade showing marginal and lateral abaxial glands (arrowed).

C, short-stalked, crateriform marginal gland, adaxial ribs and furrows and sclerenchyma girders.

D, marginal gland, girders and ribs and furrows.

E, detail of marginal gland and abaxial gland (arrowed); note that stalk cells are located in a crypt sunken below the level of the epidermis.

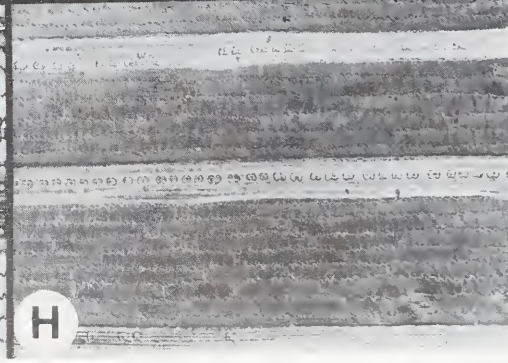
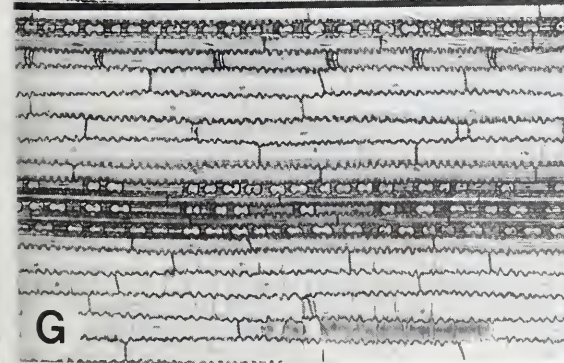
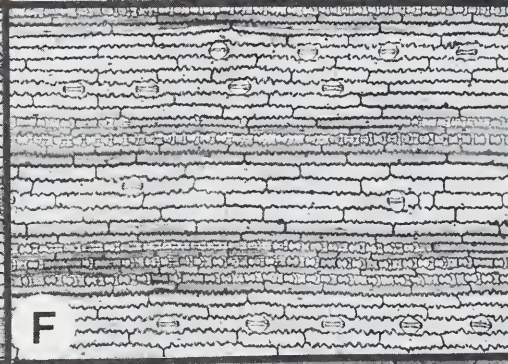
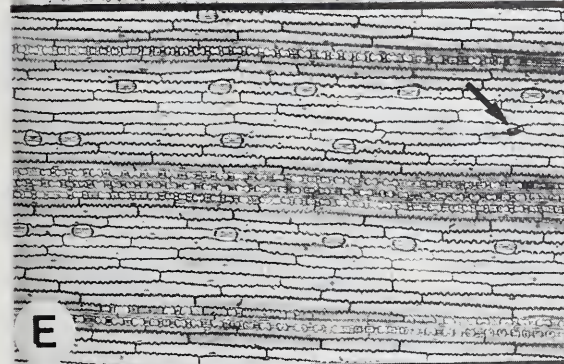
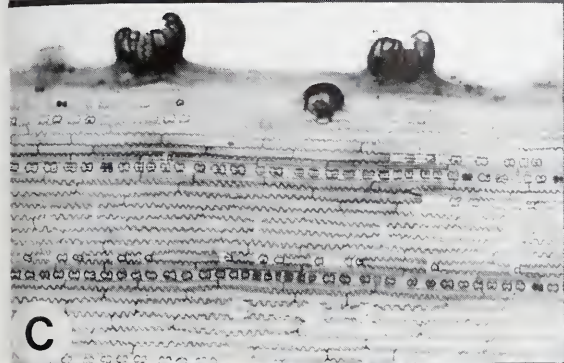
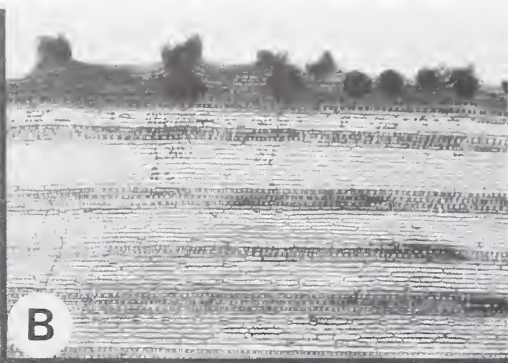
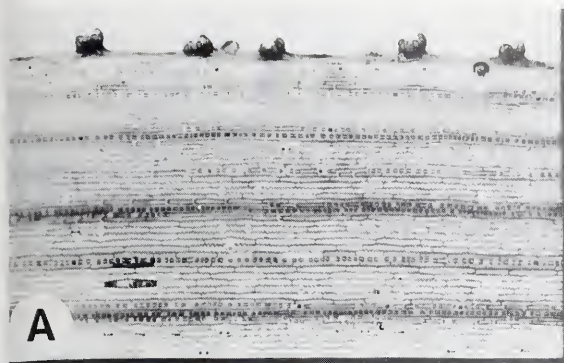
F, detail of marginal gland, narrow furrows and flat-topped ribs.

G, interference contrast of marginal gland and dense, but nevertheless diffuse, chlorenchyma of rather large angular cells. H, interference contrast showing large air spaces in chlorenchyma.

A, *Du Toit* 660; B, *Ellis* 5704; C, *Ellis* 5705; D, *Ellis* 5720; E, *Ellis* 5732; F, *Ellis* 5728; G, *Du Toit* 663; H, *Du Toit* 668; A, $\times 100$; B, $\times 160$; C–H, $\times 250$.

FIGURE 17.2.—*Pentaschistis galpinii*: abaxial epidermis.

- A, epidermal cell arrangement with laterally concentrated glands.
 - B, lateral part of blade with glands concentrated along margin and laterally on the abaxial surface.
 - C, higher magnification of marginal glands showing darkly stained collar cells.
 - D, abaxial glands located adjacent to the vascular bundles on the wide costal zones.
 - E, epidermal zonation with wide costal zones (5–7 cell files wide), intercostal long cells with undulating anticlinal walls and widely spaced stomata; rare microhair (arrowed).
 - F, epidermal cell detail.
 - G, detail of long cells with sinuous walls; note absence of stomata and irregular dumbbell-shaped silica bodies.
 - H, interference contrast of epidermis with very few stomata; note clear distinction between costal and intercostal zones and sinuous long cell walls.
- A, C, Du Toit 2288; B, Ellis 5704; D, Ellis 5732; E, Ellis 5705; F, Ellis 5694; G, Ellis 5728; H, Du Toit 660. A, B, $\times 100$; C–H, $\times 250$.



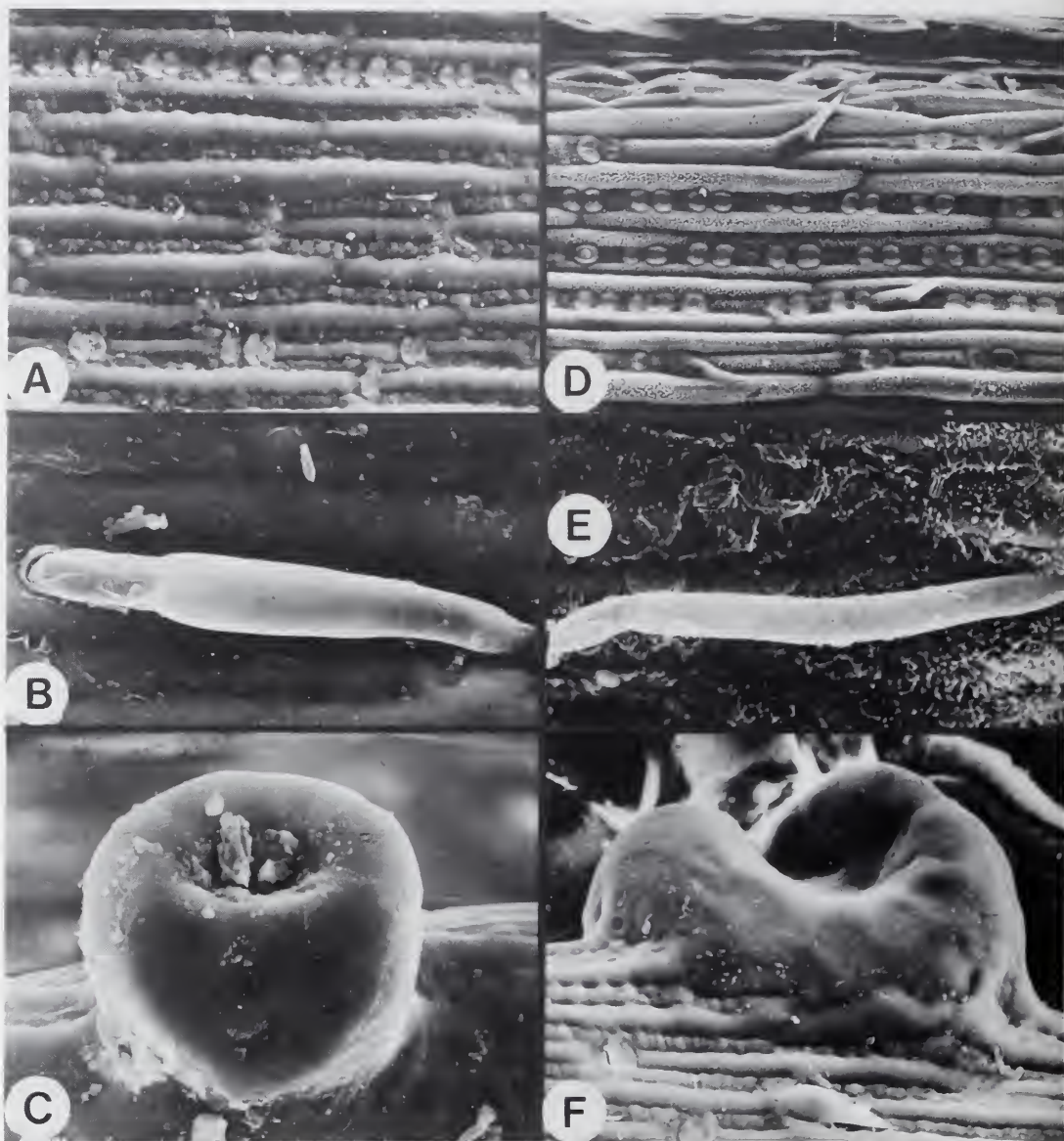


FIGURE 17.3.—*Pentaschistus galpinii*: epidermal ultrastructure. A–C, abaxial epidermis. D–F, adaxial epidermis. A, inflated periclinal and thick, sinuous anticlinal walls of intercostal long cells; note dumbbell-shaped silica bodies and absence of epidermal projections. B, rare abaxial microhair with blunt, short distal cell. C, raised, crateriform abaxial gland. D, adaxial rib with costal silica bodies and elongated long cells on sides of furrow. E, very narrow adaxial microhair with small distal cell. F, marginal gland slightly raised with crateriform apex. A, D, F, *Ellis* 5728; B, *Ellis* 5704; C, E, *Ellis* 5694. A, D, $\times 200$; F, $\times 300$; C, $\times 500$; B, E, $\times 800$.

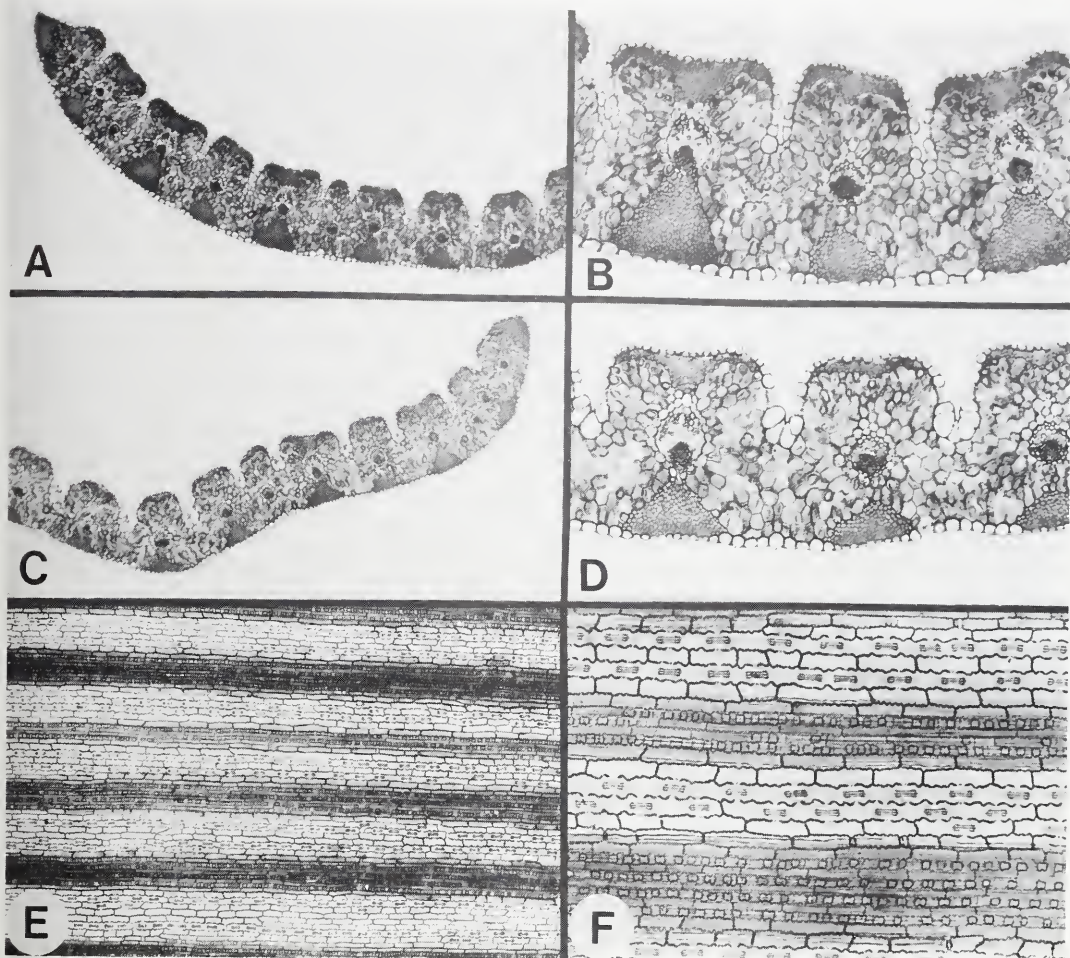


FIGURE 18.1.—*Pentaschistis microphylla*: transectional and epidermal anatomy.

A, open leaf outline; note relative thickness of blade.

B, detail of flat-topped adaxial ribs, cleft-like furrows, anchor-shaped adaxial girders and very large trapezoidal abaxial girders; mesophyll rather dense but of rather large angular cells.

C, outline showing median vascular bundle structurally undifferentiated from lateral first order bundles.

D, anatomical detail; note inconspicuous outer bundle sheath cells containing chloroplasts.

E, abaxial epidermal pattern with wide costal zones equal in width to the intercostal zones.

F, detail of wide costal zones, comprising up to 9 cell files, with irregularly dumbbell-shaped silica bodies; intercostal zones relatively narrow (5 files wide) with short, rectangular long cells with sinuous walls and numerous stomata; note absence of hairs.

A, B, E, F, *Ellis* 2592; C, D, *Ellis* 2593. A, C, E, × 100; B, D, F, × 250.

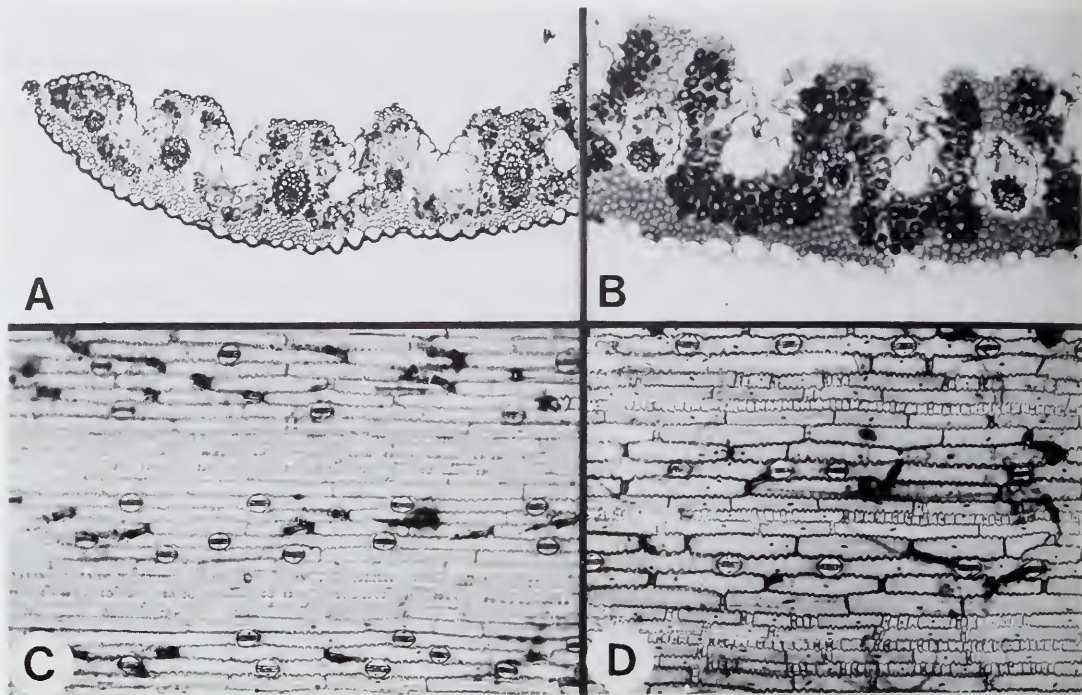


FIGURE 19.1.—*Pentaschistis ecklonii*: transectional and epidermal anatomy. A, B, transverse leaf blade sections. C, D, abaxial epidermis in surface view.
 A, leaf margin showing well-developed adaxial ribs and furrows and bulliform cell groups; note lateral fusion of abaxial sclerenchyma girders forming an almost continuous hypodermal layer.
 B, detail of compact but mesic type chlorenchyma and sclerenchyma tissue with very thick cellulose secondary walls.
 C, epidermal zonation showing stomata and microhairs in intercostal zones and wide costal zones with very irregular silica bodies.
 D, detail of irregular dumbbell-shaped silica bodies, stomata and microhairs in which the distal cells are collapsed and contain a darkly staining secretory substance.
 A–C, *Ellis 5984*; D, *Ellis 5985*. A, C, D, $\times 250$; B, $\times 400$.

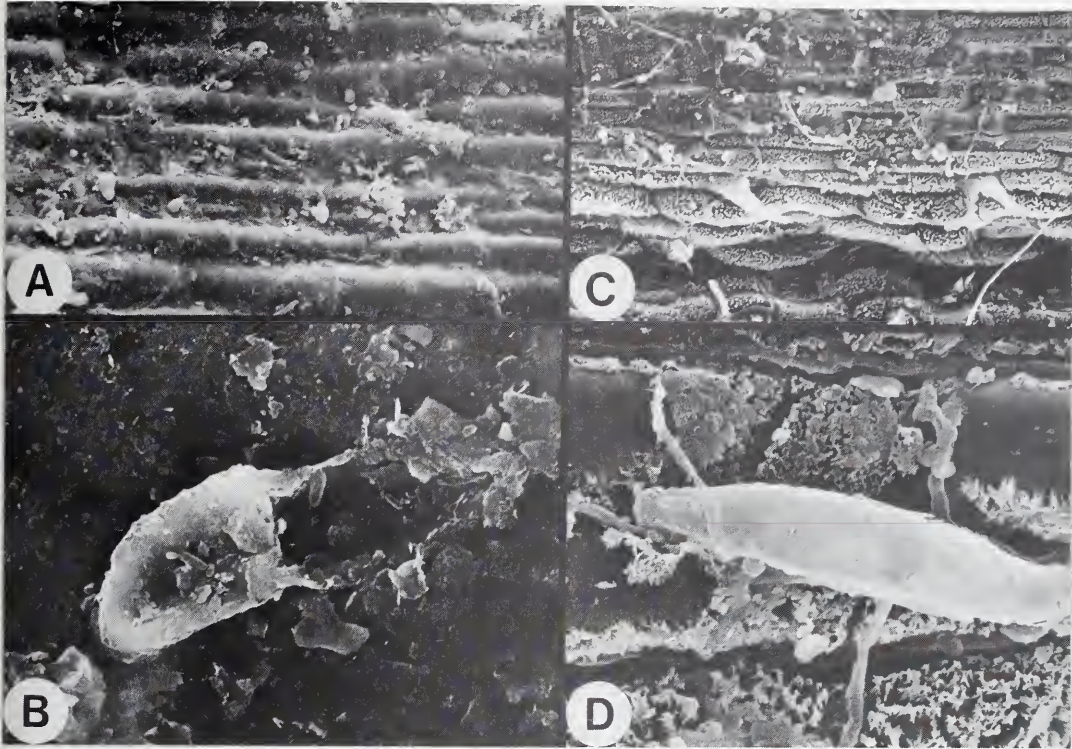


FIGURE 19.2.—*Pentaschistis ecklonii*: ultrastructure of leaf blade. A, B, abaxial epidermis. C, D, adaxial epidermis. A, featureless abaxial epidermis. B, microhair in which distal cell has collapsed; note ratio of basal and distal cells is about equal. C, adaxial rib with very small hooks. D, adaxial microhair with tapering distal cell; note fungal hyphae and well-developed epicuticular wax rods. A, C, D, *Ellis* 5984; B, *Ellis* 5985. A, C, $\times 700$; B, $\times 900$; D, $\times 1130$.

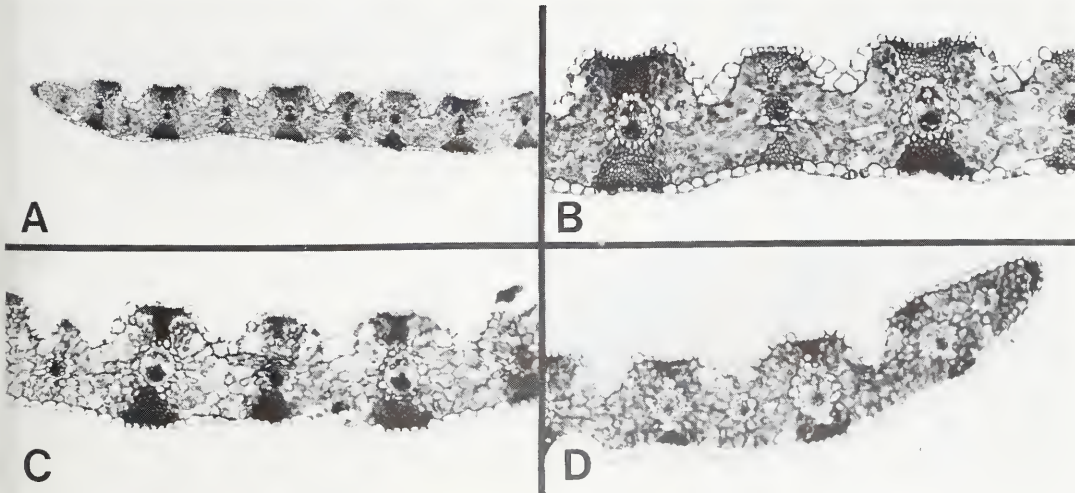


FIGURE 20.1.—*Pentaschistis reflexa*: leaf in transection. A, open, expanded outline. B, anatomical detail of diffuse mesophyll and well-developed sclerenchyma girders. C, cross sectional anatomical structure. D, lateral part of blade with slightly tapering margin. A, B, *Ellis* 5579; C, *Ellis* 5578; D, *Ellis* 5786. A, $\times 100$; B–D, $\times 250$.

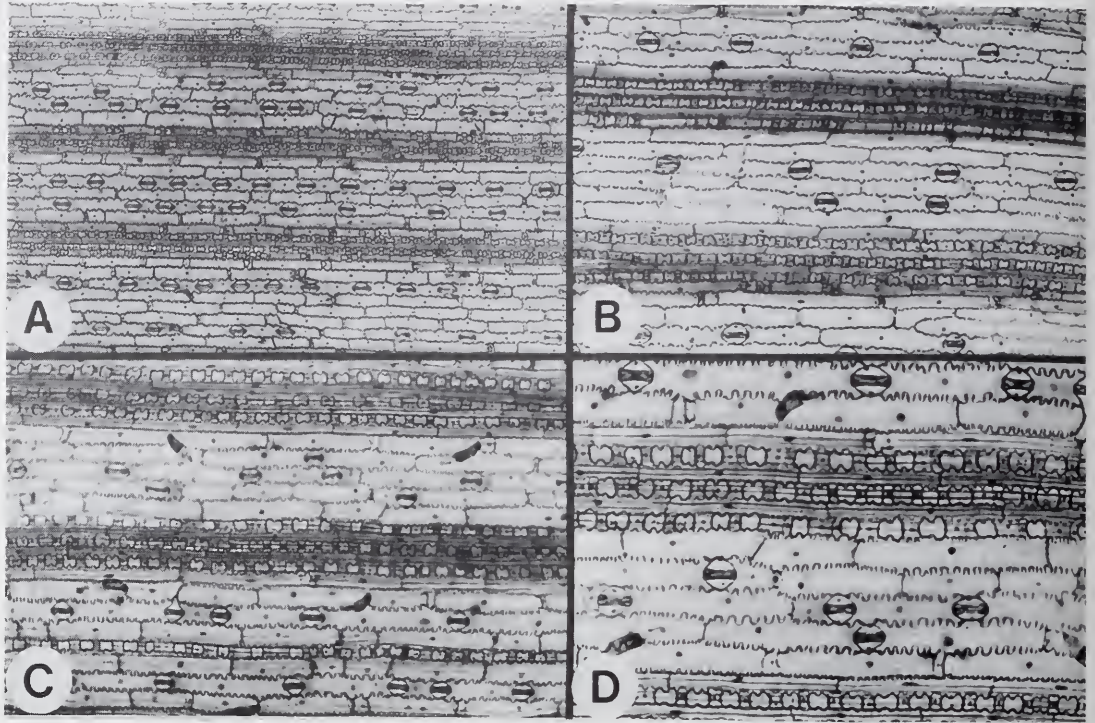


FIGURE 20.2.—*Pentaschistis reflexa*: abaxial epidermis.

A, epidermal zonation.

B, detail of long cells and domed stomata and dumbbell-shaped silica bodies.

C, epidermal pattern; note numerous microhairs.

D, detail of sinuous-walled long cells, domed stomata, microhairs and shortly dumbbell-shaped silica bodies.

A, Ellis 5786; B, Ellis 5579; C, D, Ellis 5578. A, $\times 160$; B, C, $\times 250$; D, $\times 400$.

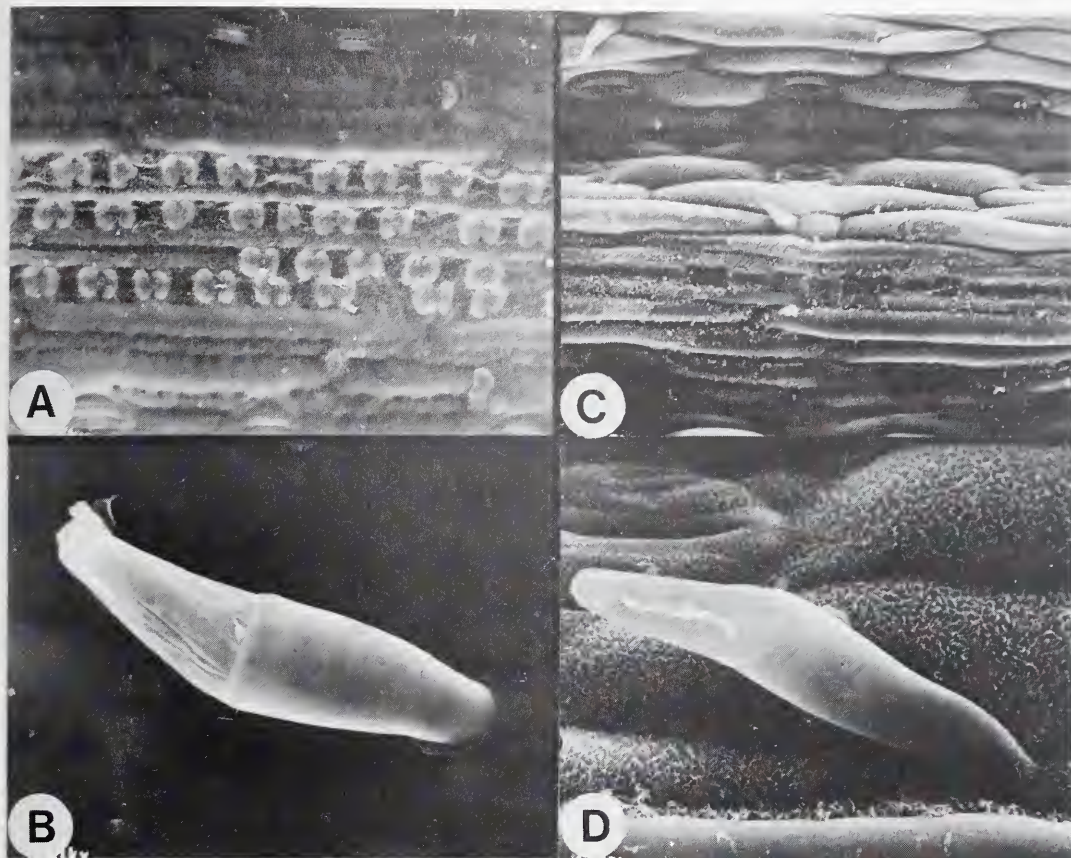


FIGURE 20.3.—*Pentaschistis reflexa*: epidermal ultrastructure. A, B, abaxial epidermis. C, D, adaxial epidermis. A, costal zone with dumbbell-shaped silica bodies. B, microhair with tapering distal cell equal in length to basal cell. C, adaxial rib and furrow with minute prickles hairs. D, adaxial microhair with basal cell longer than distal cell. A–D, *Ellis 5578*. A, C, $\times 200$; B, D, $\times 1000$.

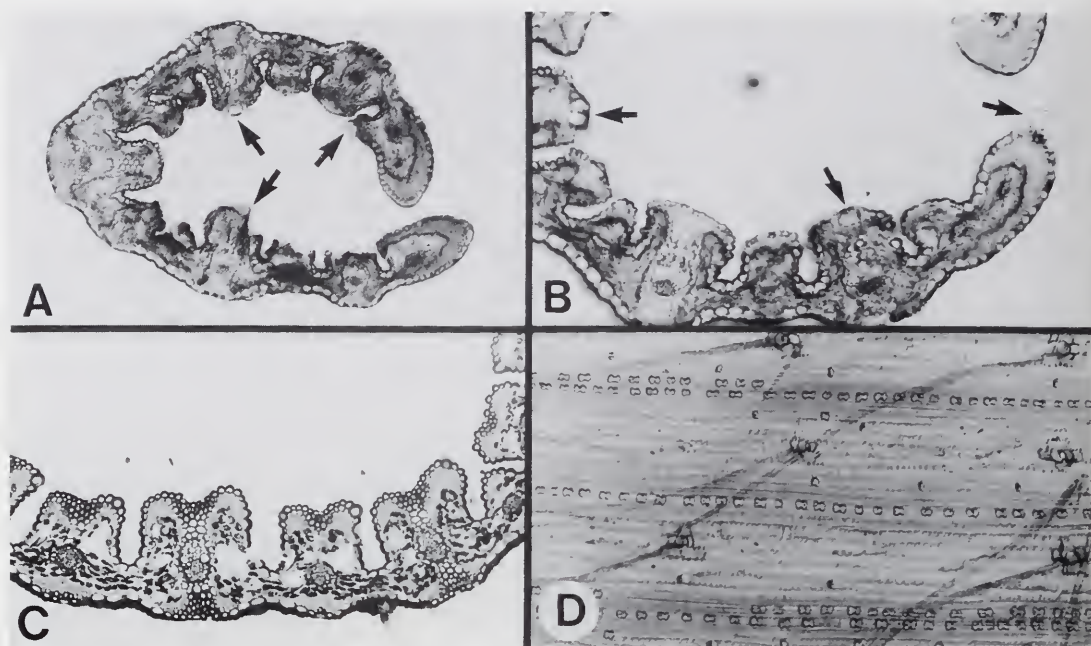


FIGURE 21.1.—*Pentaschistis borussica*: leaf in cross section and abaxial epidermis.

A, rather narrow infolded blade; note sessile glands adaxially located (arrowed).

B, detail of sessile glands on ribs and margin; note large adaxial ribs and prominent sclerenchyma girders and cap in blunt margin.

C, wide, expanded blade with massive, flat-topped adaxial ribs and cleft-like furrows; no adaxial glands visible.

D, abaxial epidermis showing absence of stomata, long, very thin macrohairs inserted into a few modified and inflated epidermal cells and very long basal cells of microhairs.

A, B, *Rauh* 145; C, D, *Goyns* 15. A, $\times 160$; B–D, $\times 250$.

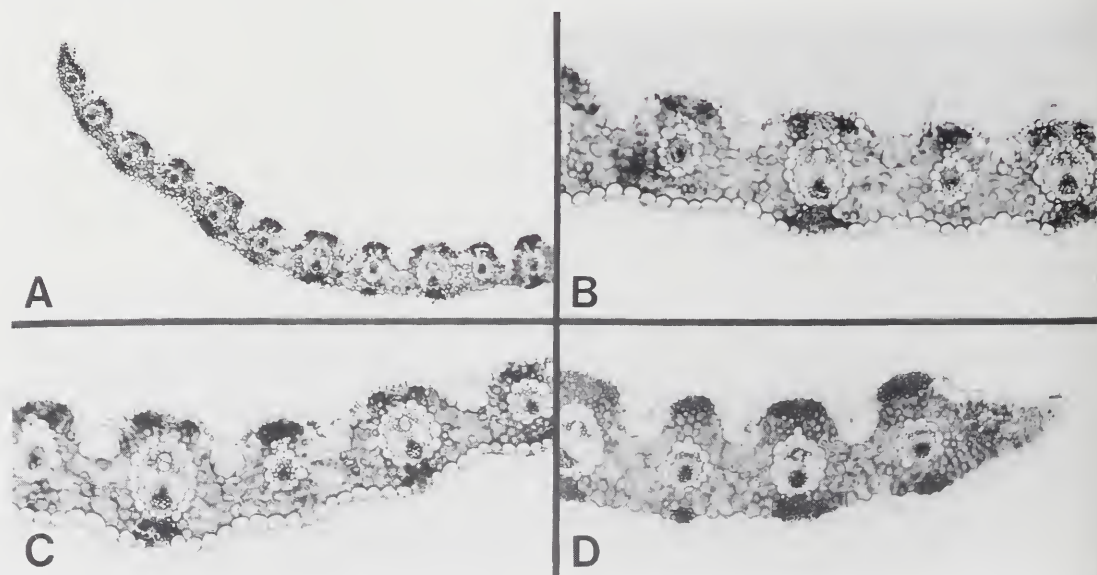


FIGURE 22.1.—*Pentaschistis natalensis*: crosssectional leaf anatomy.

A, expanded, open leaf outline.

B, detail of shallow abaxial and adaxial ribs and furrows, diffuse chlorenchyma, translucent bundle sheath cells and abaxial sclerenchyma girders associated only with first order vascular bundles; cuticle relatively thick.

C, structural detail very similar to that of B; note absence of abaxial stomata.

D, characteristic tapering margin extended into a pointed projection.

A, B, *Ellis* 5736; C, *Ellis* 5737; D, *Ellis* 225. A, $\times 100$; B–D, $\times 250$.

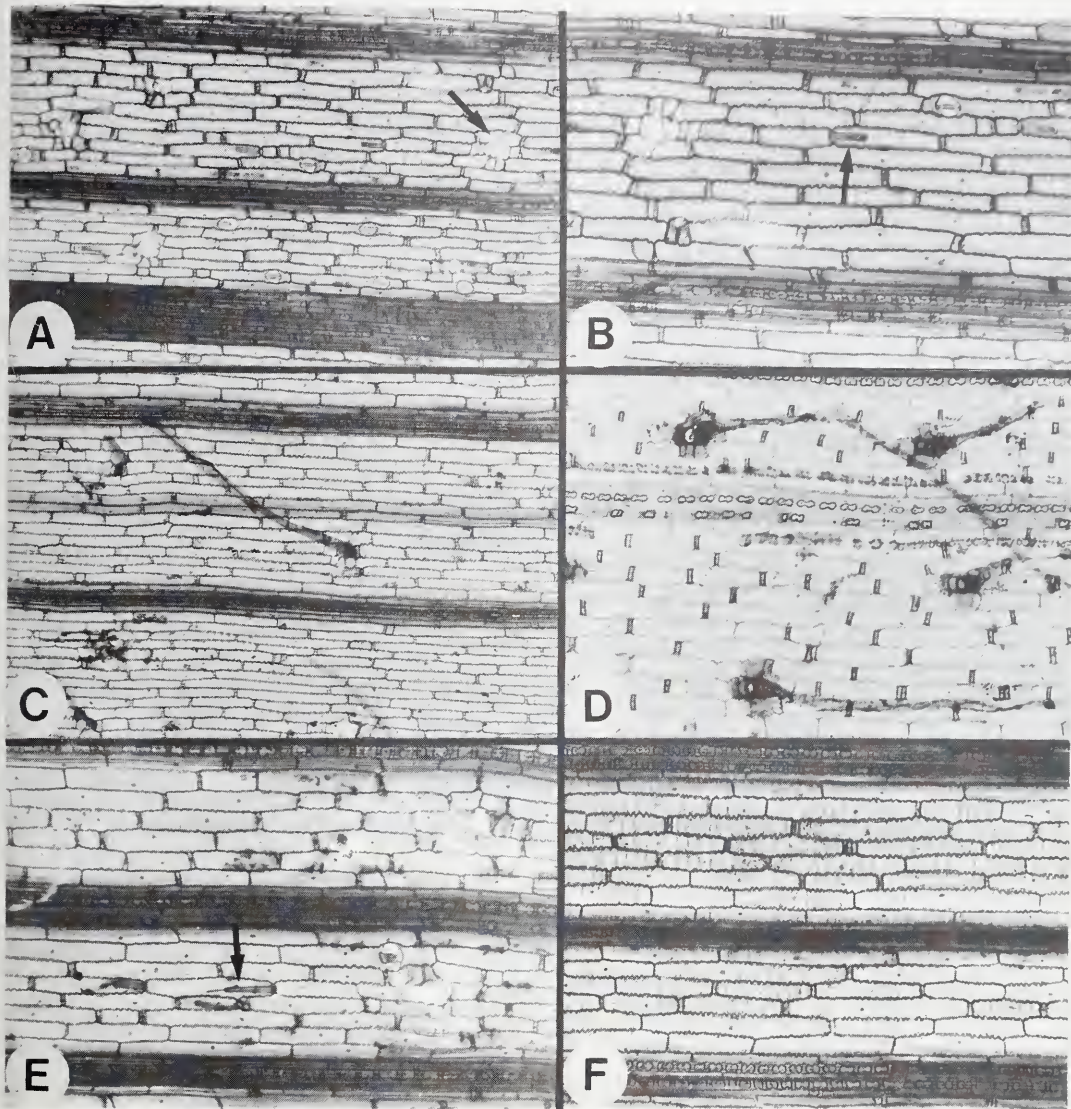


FIGURE 22.2.—*Pentaschistis natalensis*: abaxial epidermis.

A, epidermal zonation with clearly differentiated costal and intercostal zones; note modified cells associated with macrohair bases (arrowed).

B, detail of long cells separated by tall and narrow short cells, very irregularly shaped silica bodies and microhairs (arrowed); note that abaxial stomata are uncommon and deformed.

C, epidermal zonation with macrohairs visible.

D, detail of flexible macrohairs with swollen bases inserted between a few modified epidermal cells; note intercostal short cells, silica bodies and absence of stomata.

E, detail of microhairs (arrowed), deformed stoma and macrohair basal cells.

F, abaxial epidermis without stomata; silica bodies of the dumbbell-shaped type.

A, B, Ellis 5736; C, Ellis 5737; D, Ellis 1542; E, Ellis 5735; F, Ellis 4461. A, C, $\times 160$; B, D–F, $\times 250$.

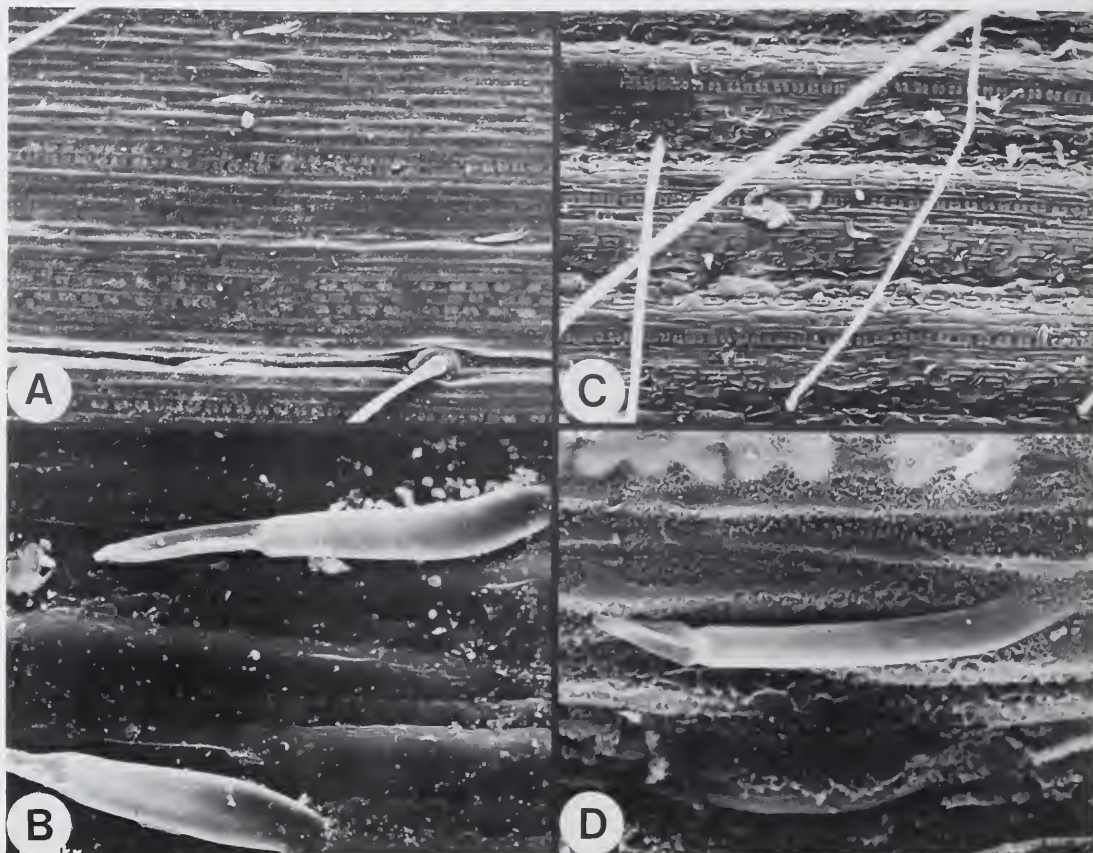


FIGURE 22.3.—*Pentaschistis natalensis*: SEM of leaf blade surface. A, B, abaxial epidermis. C, D, adaxial epidermis. A, abaxial epidermal structure with macrohair, microhairs and clearly differentiated costal and intercostal zones. B, abaxial microhairs with tapering distal cells shorter than the basal cells. C, adaxial ribs and furrows and macrohairs. D, adaxial microhair with very short, tapering distal cell. A, B, D, *Ellis 446l*; C, *Ellis 5735*. A, C, $\times 60$; B, $\times 550$; D, $\times 700$.

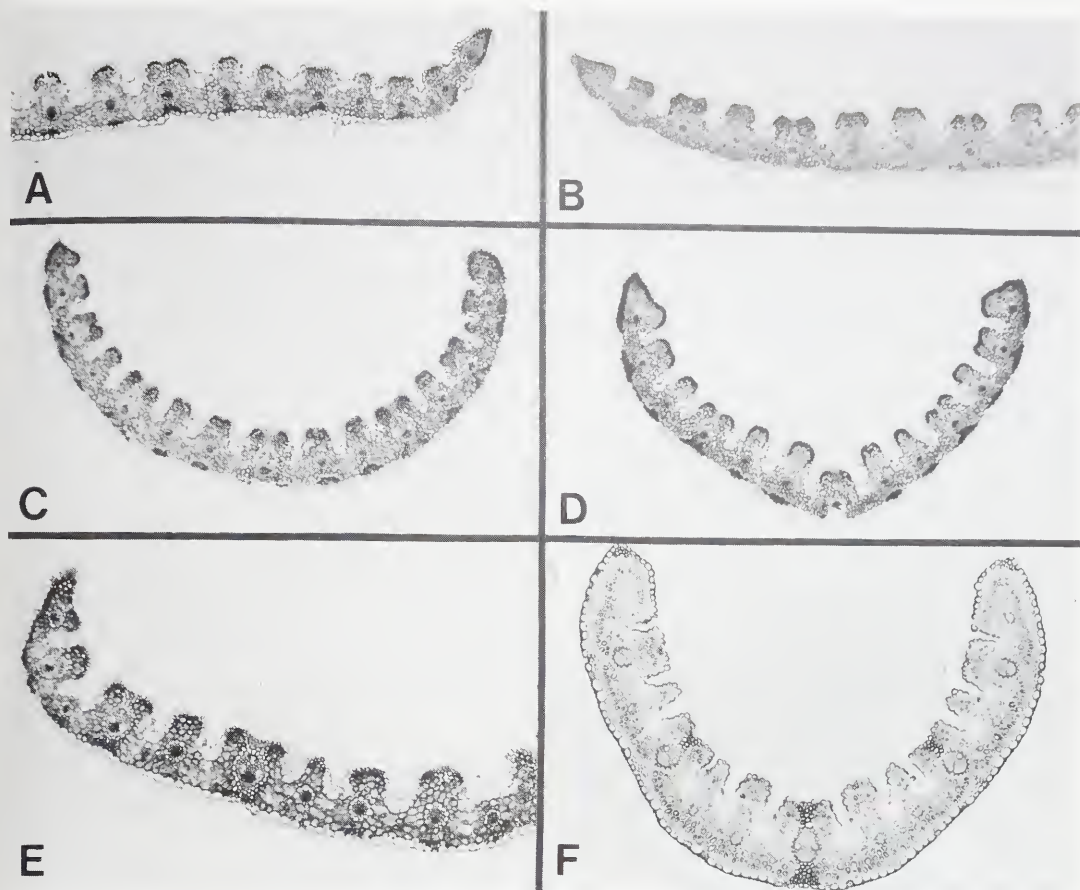


FIGURE 23.1.—*Pentaschistis oreodoxa*: variation in leaf outline; specimens without marginal glands used for comparative purposes.

A, open, expanded leaf blade with only small sclerenchyma girders associated with the vascular bundles.

B, open, flat blade in which sclerenchyma girders are better developed than in A.

C, slightly inrolled outline with sclerenchyma girders tending to fuse, particularly laterally; note that adaxial furrows are narrower than in the expanded blades.

D, blade with infolded outline and sclerenchyma girders spreading laterally but not fused to form hypodermal layer.

E, notice relative width and leaf thickness of expanded blade without fused abaxial sclerenchyma girders; compare with F.

F, narrow, inrolled, relatively thick blade of specimen with continuous hypodermal sclerenchyma layer.

A, Ellis 5729; B, Du Toit 664; C, Ellis 5731; D, Ellis 5721; E, Ellis 5718; F, Du Toit 645. A–D, $\times 100$; E, F, $\times 160$.

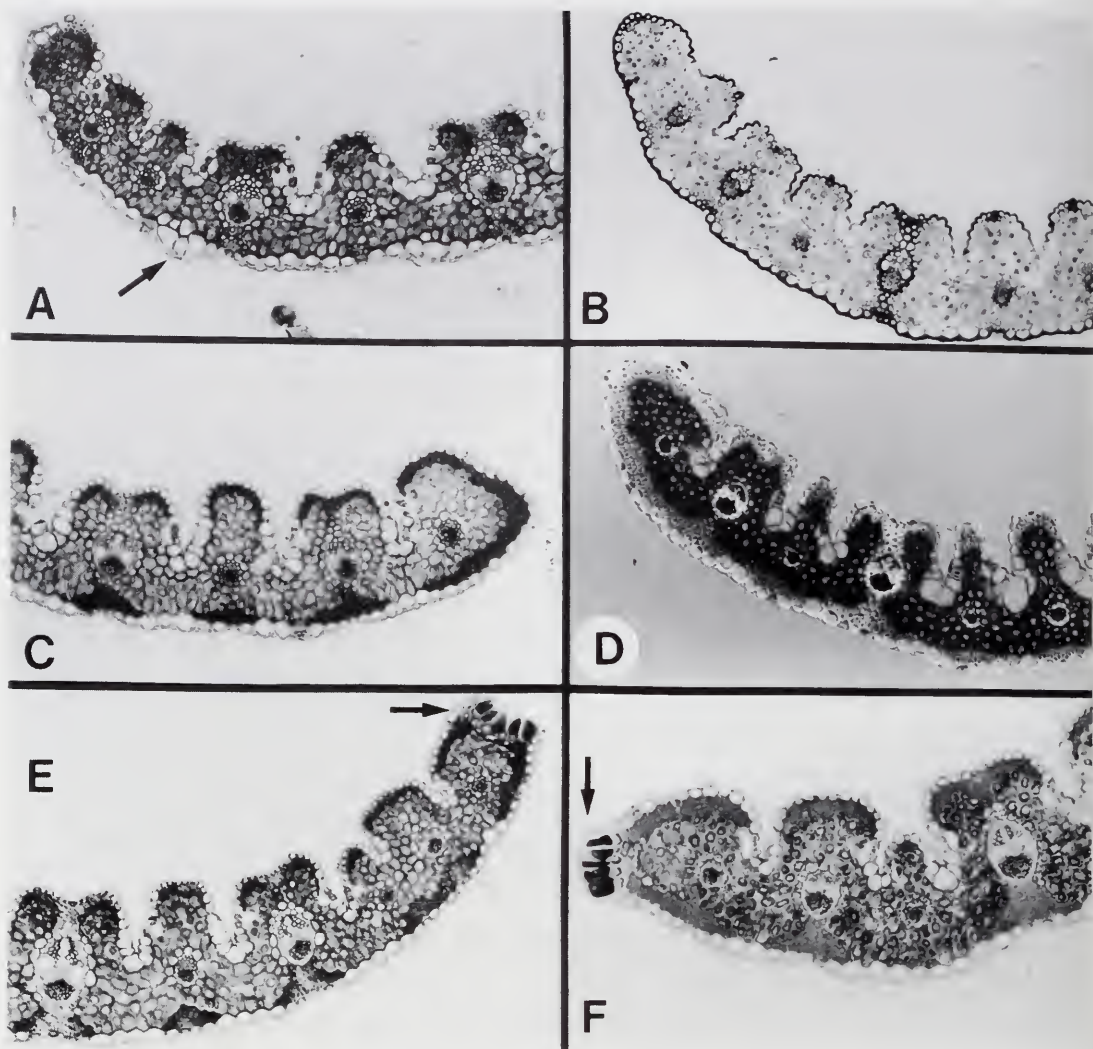


FIGURE 23.2.—*Pentaschistis oreodoxa*: detail of transectional leaf anatomy.

A, mesic anatomy with thick, continuous abaxial cuticle; abaxial sclerenchyma girders very small; note cushion base cells of macrohairs (arrowed).

B, lateral part of blade of specimen with small abaxial sclerenchyma girders; note stained nuclei in chlorenchyma cells.

C, lateral part of blade with fused abaxial sclerenchyma girders, particularly around the margin.

D, abaxial sclerenchyma girders fused to form continuous hypodermal sclerenchyma layer.

E, crateriform gland without stalk located in leaf margin (arrowed); note darkly staining gland cells and unstained collar cells.

F, sessile marginal gland (arrowed).

A, Ellis 5722; B, Ellis 5707; C, Ellis 5721; D, Du Toit 645; E, Ellis 5731; F, Ellis 3132. A–F, $\times 250$.

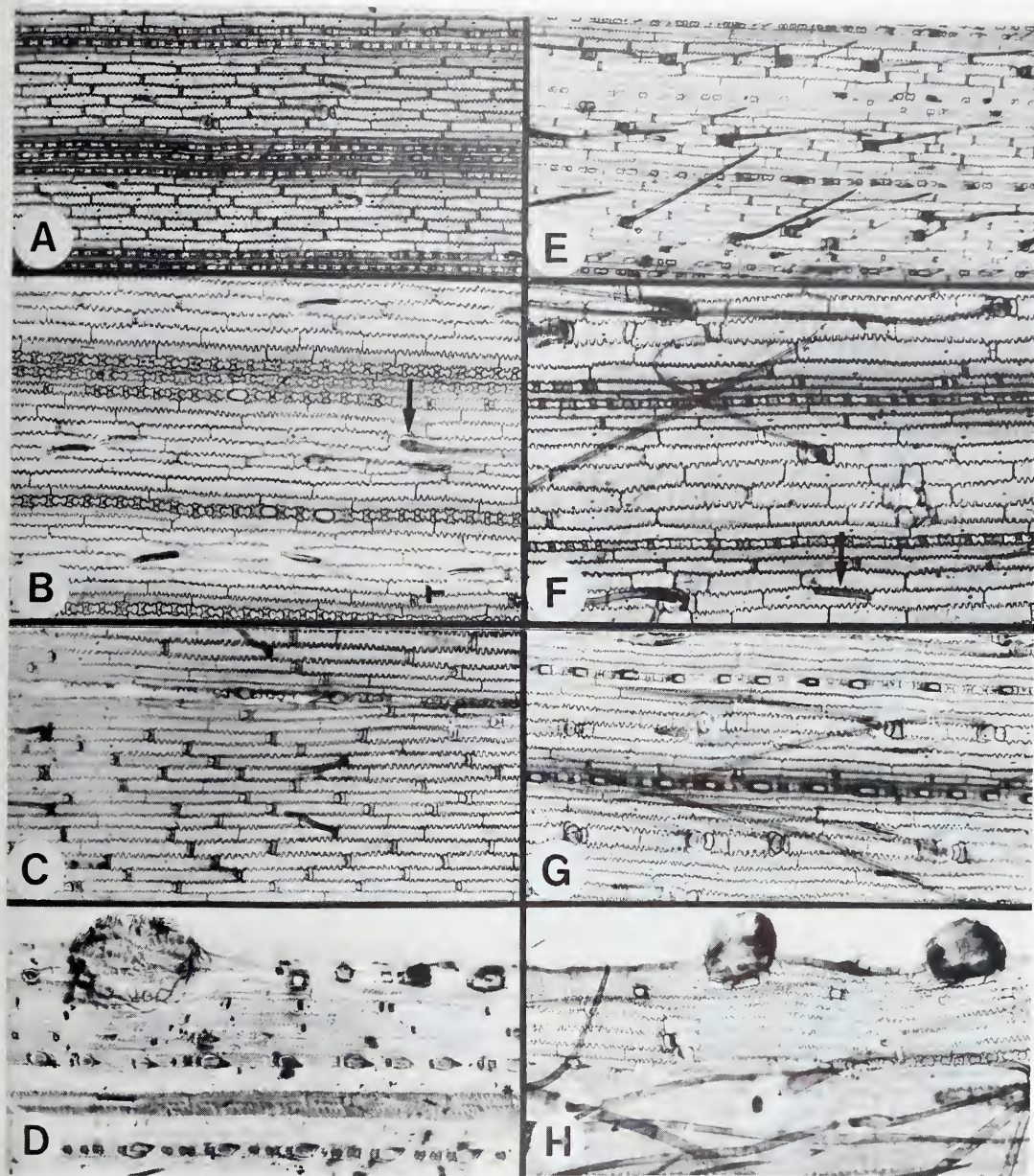


FIGURE 23.3. — *Pentaschistis oreodoxa*: abaxial epidermal structure. A–D, specimens with few or no macrohairs. E–H, pubescent specimens with macrohairs. Note all specimens without abaxial stomata, irrespective of degree of development of hypodermal sclerenchyma layer.

A, epidermal pattern and zonation; costal and intercostal zones clearly distinct.

B, detail of similar epidermis to A with uncommon macrohairs (arrowed), elongated microhairs and thick, undulating long cell walls; note dumbbell-shaped silica bodies and costal prickly hairs.

C, common microhairs with long basal cells, successive long cells in a file separated by cork-silica cell pairs and costal prickles present.

D, margin with slightly raised marginal gland; note numerous prickly hairs.

E, leaf with numerous short, stiff macrohairs with bases inserted between one or two inflated epidermal cells.

F, detail of macrohairs and inflated epidermal cells associated with the hair bases; note extremely elongated basal cell of microhair (arrowed).

G, numerous macrohairs, many costal prickles and elongated microhairs, all characteristic of this species.

H, leaf margin with raised, domed glands; note numerous macrohairs.

A, *Ellis 5731*; B, *Ellis 5721*; C, *Ellis 1403*; D, *Ellis 1407*; E, *Killick & Vahrmeijer 3992*; F, *Ellis 5729*; G, *Ellis 5707*;

H, *Du Toit 2291*. A, E, $\times 160$; B–D, F–H, $\times 250$.

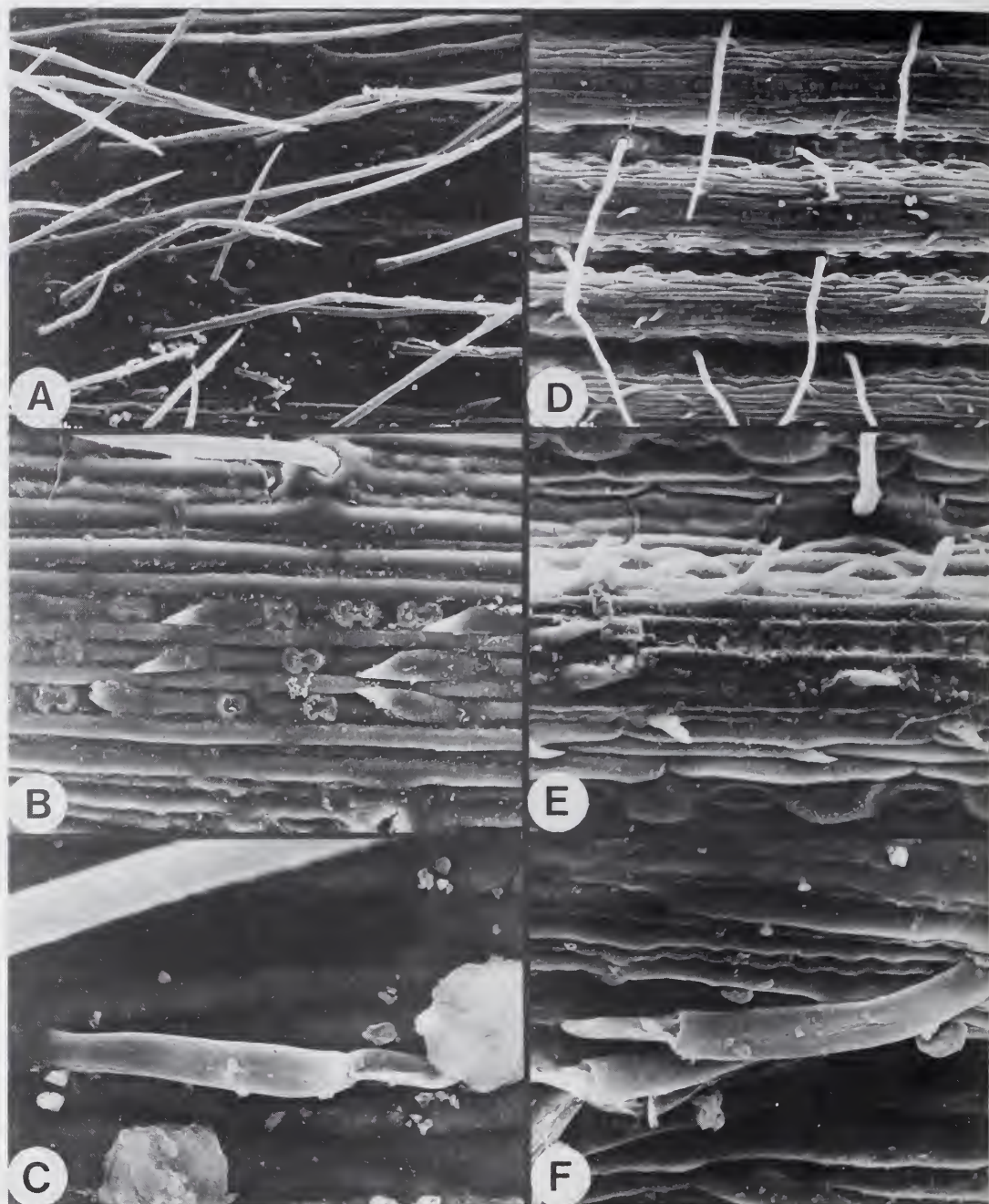


FIGURE 23.4.—*Pentaschistis oreodoxa*: leaf blade ultrastructure. A–C, abaxial epidermis. D–F, adaxial epidermis. A, epidermal cell arrangement with numerous stiff macrohairs. B, more detail of abaxial surface showing macrohair and slightly raised base, costal prickles and silica bodies and thick-walled intercostal long cells. C, microhair with very short distal cell. D, adaxial surface cell arrangement; note ribs and furrows and intercostal macrohairs. E, more detail of cells of adaxial rib with small prickles and stomata and macrohair located at base of furrow. F, adaxial microhairs also with elongated basal cell and very short distal cell. A, C, D, Ellis 5729; B, Ellis 5707; E, Ellis 5718. A, D, $\times 60$; B, E, $\times 200$; C, F, $\times 530$.

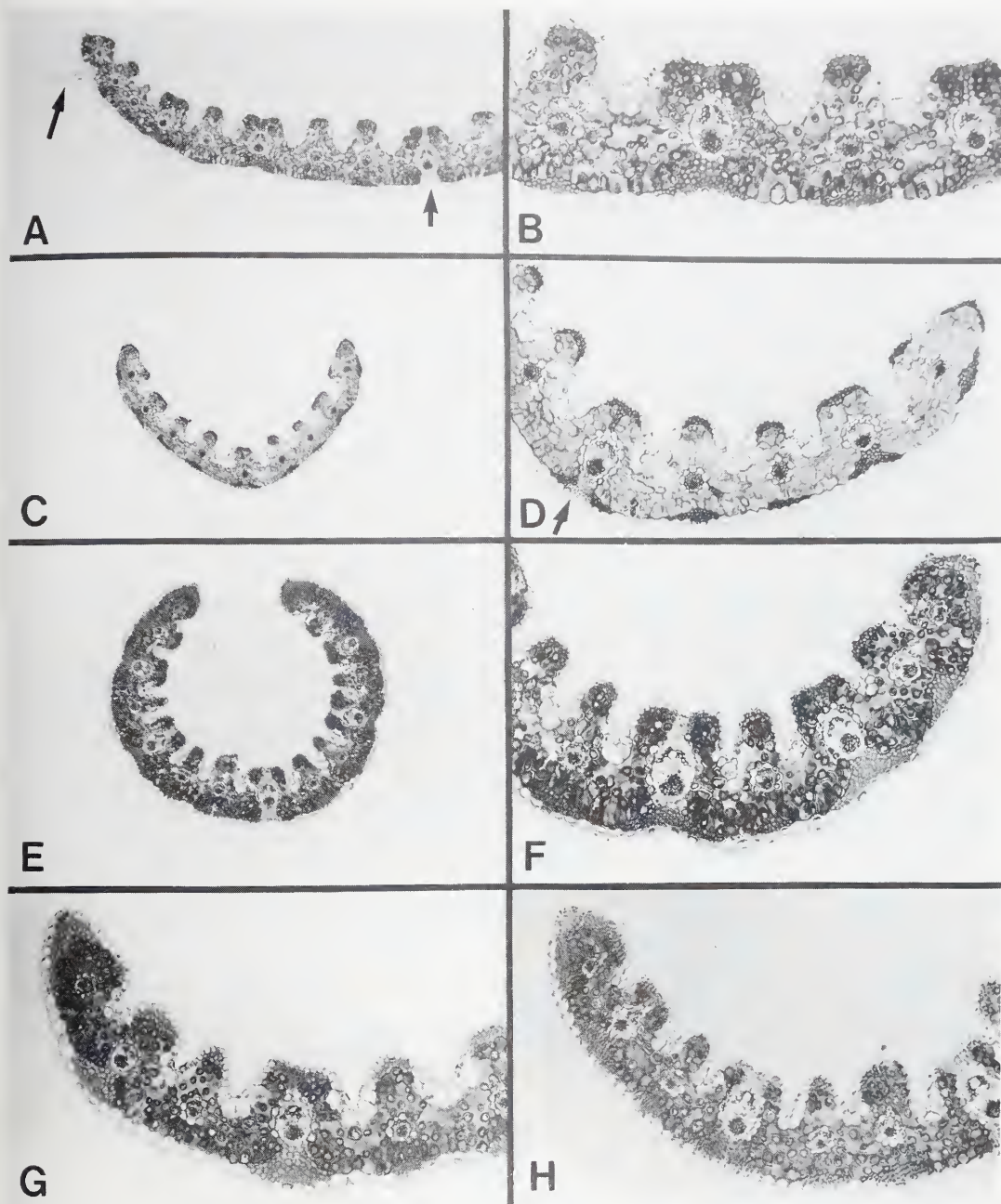


FIGURE 24.1.—*Pentaschistis setifolia*: leaf blade transections of specimens without sunken glands.

A, open, expanded blade outline; note macrohair base (arrowed); median vascular bundle distinguishable only by lignified girder sclerenchyma tissue (arrowed).

B, anatomical detail of diffuse chlorenchyma tissue and parenchyma sheath cells with chloroplasts.

C, outline of narrow, infolded blade.

D, detail showing lignification of girder associated with the median bundle (arrowed).

E, inrolled outline.

F, anatomical detail.

G, detail of lateral part of blade showing well-developed ribs and furrows.

H, interference contrast of abrupt margin.

A, B, *Ellis* 2596; C, D, *Ellis* 5684; E, F, *Ellis* 2601; G, *Ellis* 2377; H, *Ellis* 2377. A, C, E, $\times 100$; B, D, F–H, $\times 250$.

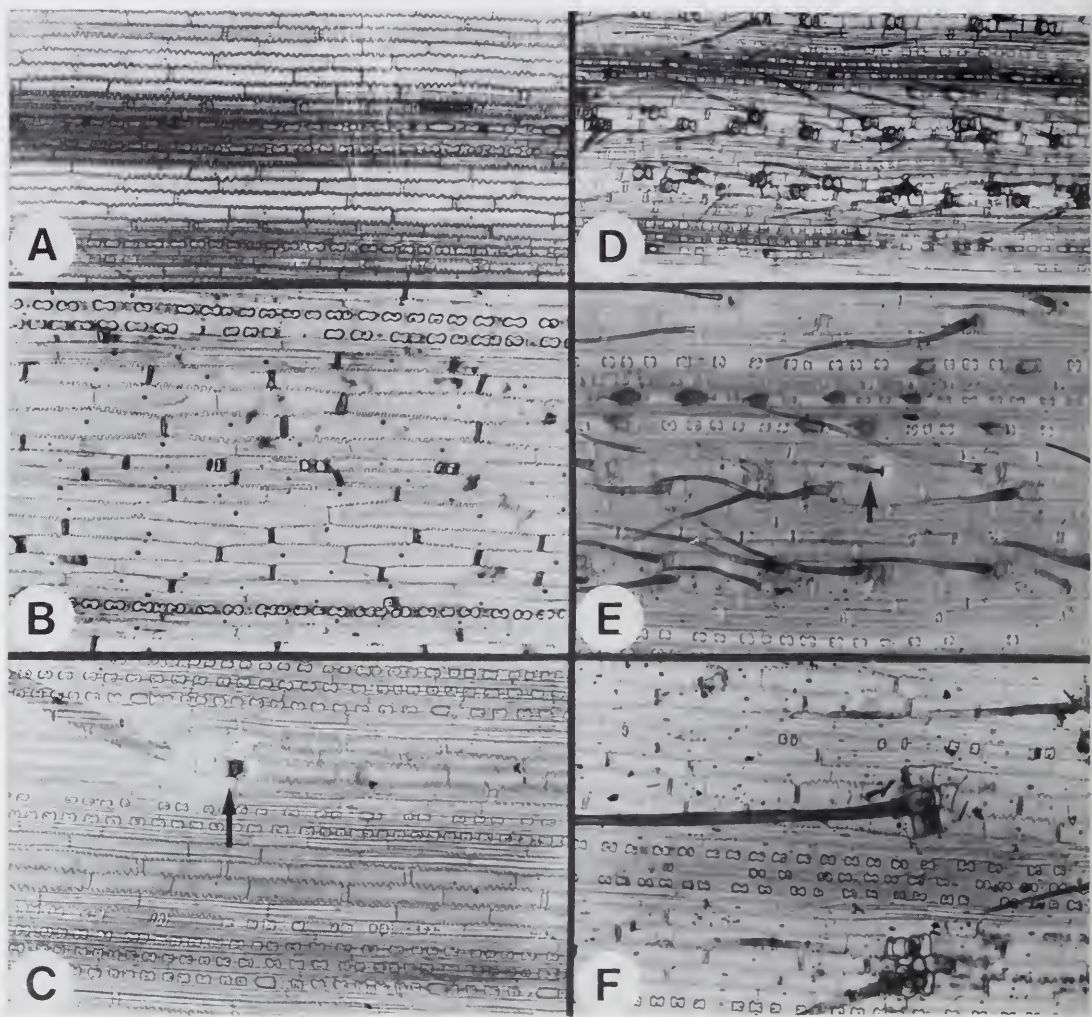


FIGURE 24.2.—*Pentaschistis setifolia*: abaxial epidermis of specimens without sunken glands. A–C, specimens without macrohairs. D–F, specimens with macrohairs.

A. costal and intercostal zonation; note dumbbell-like silica bodies and thick, sinuous, long cell walls; stomata, prickles, microhairs and macrohairs absent.

B. sinuous walls of slightly hexagonal long cells all separated by a single, tall and narrow short cell; no stomata, prickles or microhairs.

C. specimen with few, thick, very elongate macrohairs with base arrowed; note few small costal prickles.

D. zonation of leaf with numerous short macrohairs with single inflated epidermal cell associated with the base.

E. detail of D showing macrohairs, microhairs (arrowed) and prickles; note absence of stomata.

F. detail of elongated macrohair bases and silica bodies.

A, *Ellis* 5684; B, *Ellis & Loxton* 985; C, *Ellis* 2389; D, E, *Ellis* 2601; F, *Ellis* 2380. A, D, $\times 160$; B, C, E, F, $\times 250$.

FIGURE 24.3.—*Pentaschistis setifolia*: transverse sections of specimens with sunken and raised glands.

A. sunken glands (arrowed) located in the costal zones adjacent to the vascular bundles.

B. sunken glands in margin and opposite vascular bundles (arrowed).

C. detail of sunken glands (arrowed) and abrupt margin.

D. sunken glands (arrowed) and abrupt margin.

E. detail of sunken glands, parenchyma sheath cells with chloroplasts and large, angular and rather dense chlorenchyma.

F. detail of marginal sunken gland showing gland and collar cells.

G. short-stalked marginal gland.

H. marginal and adaxial sessile glands (arrowed).

A, C, *Ellis* 2612; B, *Ellis* 2614; D, *Ellis* 5692; E, *Ellis* 2611; F, *Ellis* 5818; G, *Ellis* 3301; H, *Ellis* 5693. A, B, $\times 160$; C, D, G, H, $\times 250$; E, F, $\times 400$.

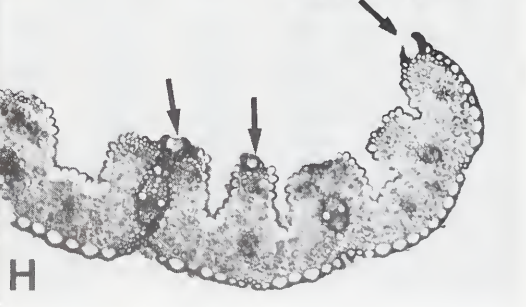
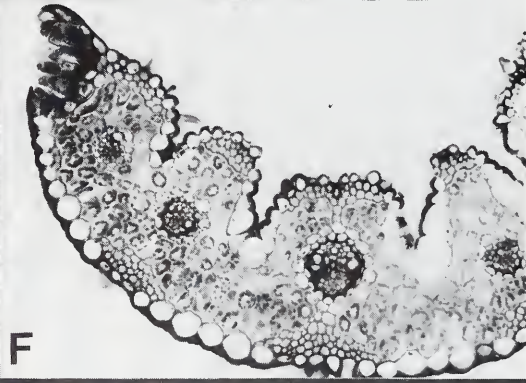
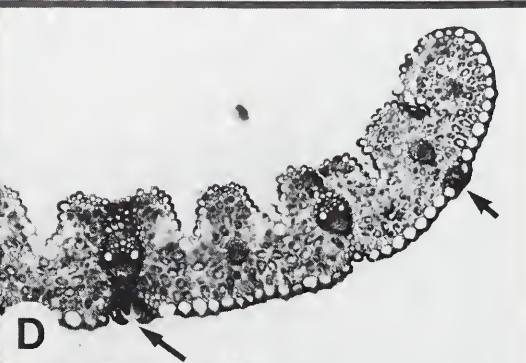
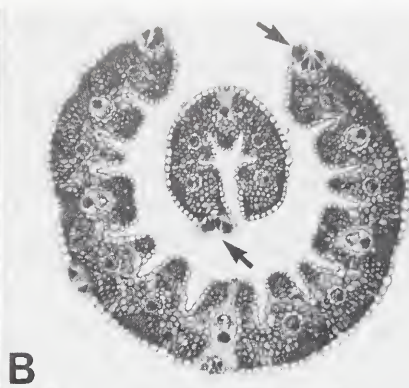
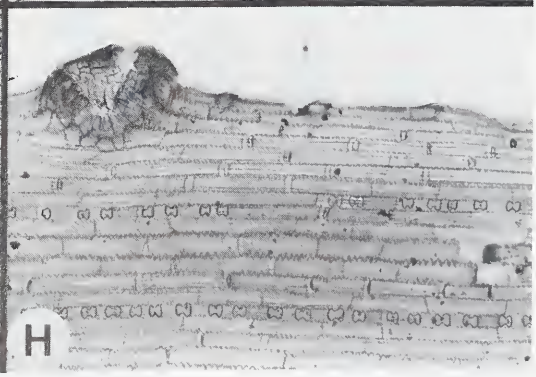
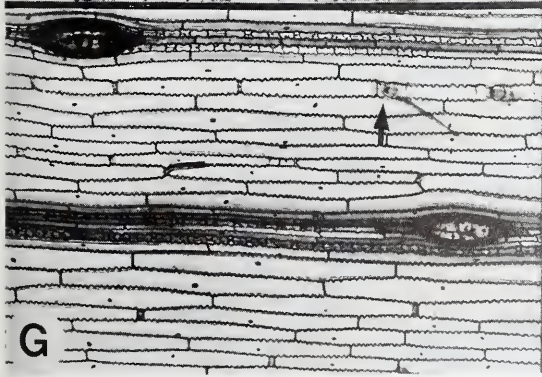
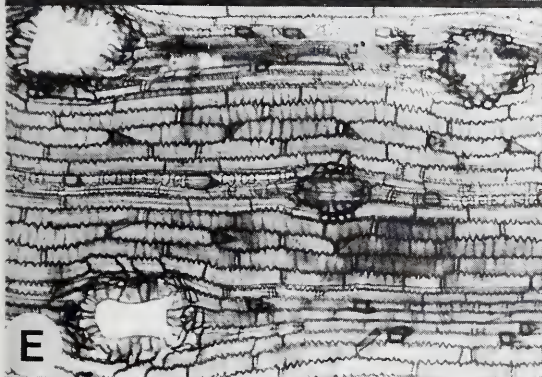
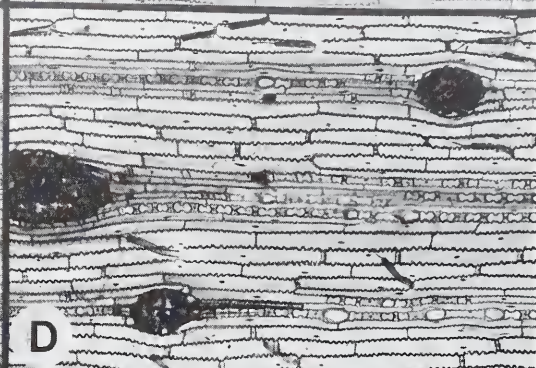
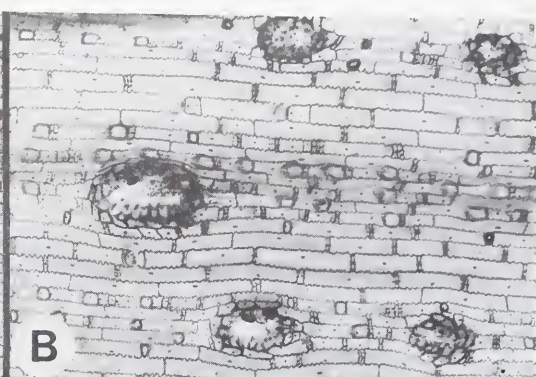
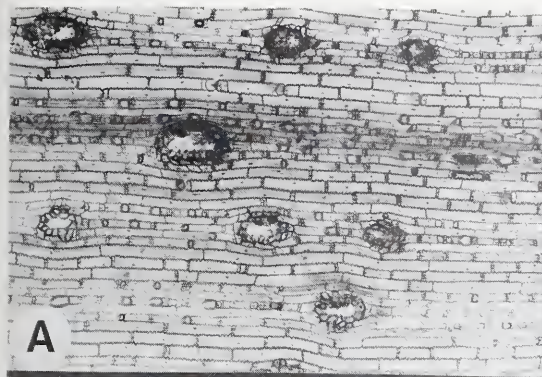
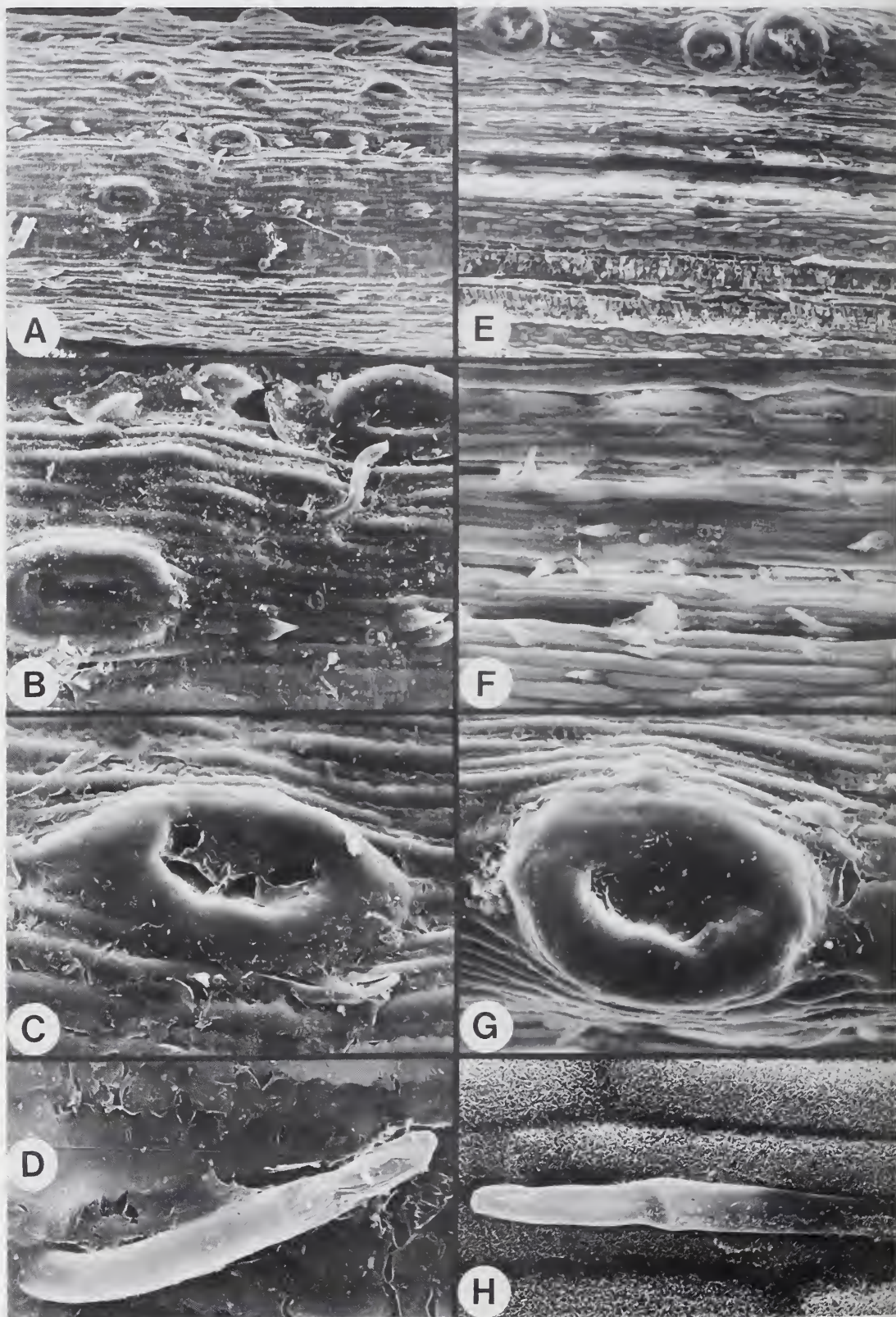


FIGURE 24.4.—*Pentascistis setifolia*: abaxial epidermis of specimens with sunken abaxial glands and slightly raised marginal glands.

- A. epidermal pattern of specimen with numerous sunken glands; note presence of costal prickles and absence of stomata and macrohairs.
 - B. detail of glands, prickles and long cells; note absence of stomata and macrohairs.
 - C. short-stalked glands on margin and sunken glands along costal zones.
 - D. sunken gland cell structure with persistent nuclei in glandular cells; note microhairs and prickles.
 - E. detail of collar cells surrounding sunken glandular cells; note presence of costal and intercostal prickles and microhairs.
 - F. differential staining of collar cells.
 - G. elongated, slightly raised glands which appear to be intermediate between the sunken and sessile types; note single microhair and bases of two macrohairs (arrowed).
 - H. detail of raised, marginal gland with collar and gland cells clearly differentiated.
- A, B, *Ellis* 5697; C, D, *Ellis* 5693; E, *Ellis* 2611; F, *Ellis* 2612; G, *Ellis* 5692; H, *Ellis* 2388. A, C, $\times 160$; B, D–H, $\times 250$.





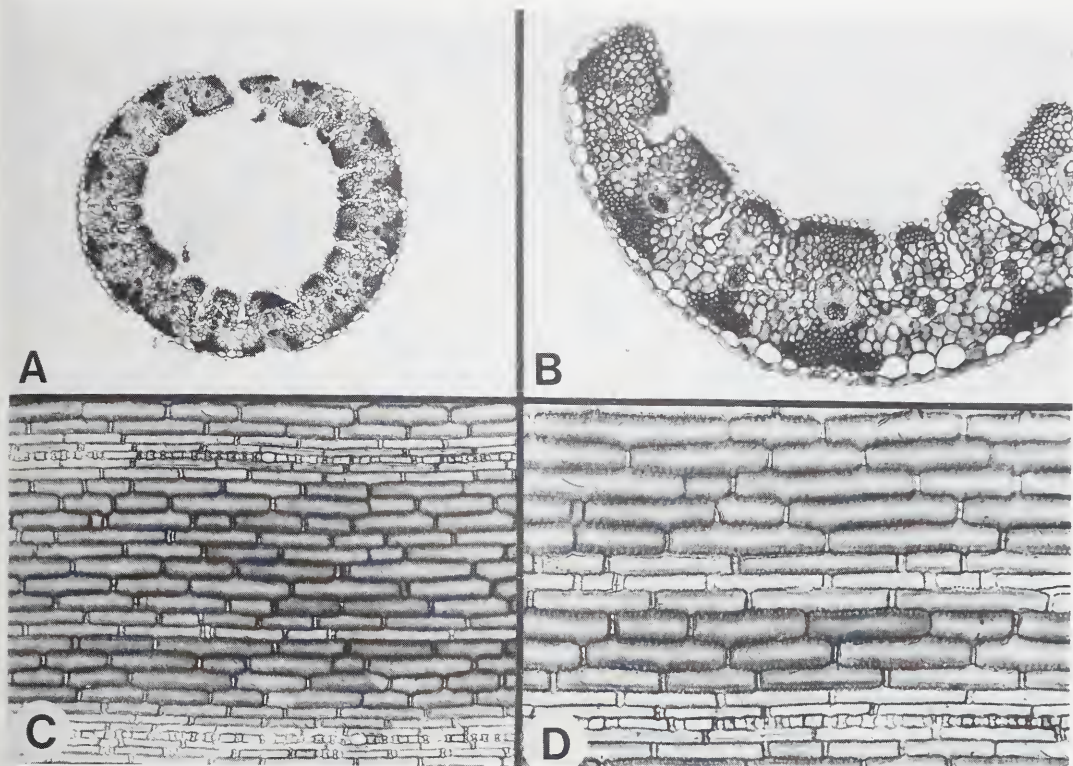


FIGURE 25.1.—*Pentaschistis ampla*: transectional and epidermal anatomy.

A, inrolled leaf outline.

B, detail of lateral part of blade with abrupt margin, deep, cleft-like adaxial furrows, sclerenchyma girders and diffuse mesophyll; note thickness of abaxial cuticle.

C, epidermal zonation showing distinction between costal and intercostal zones.

D, epidermal detail with irregularly dumbbell-shaped costal silica bodies and short, somewhat hexagonal intercostal long cells; note absence of abaxial stomata and all types of epidermal appendages.

A–D, *Ellis 559l*. A, $\times 100$; C, $\times 160$; B, D, $\times 250$.

FIGURE 24.5.—*Pentaschistis setifolia*: epidermal ultrastructure. A–D, abaxial epidermis. E–H, adaxial epidermis.

A, general view of abaxial surface.

B, raised rims of sunken glands, microhair and prickles.

C, detail of sunken gland with collar cells overarchng the gland pit.

D, abaxial microhair with distal cell shorter than basal cell.

E, adaxial surface with marginal glands.

F, adaxial surface with ribs and furrows.

G, detail of slightly raised marginal gland.

H, adaxial microhair with distal cell only slightly shorter than the basal cell.

A–H, *Ellis 5693*. A, E, $\times 60$; B, F, $\times 200$; C, G, $\times 300$; D, $\times 900$; H, $\times 1000$.

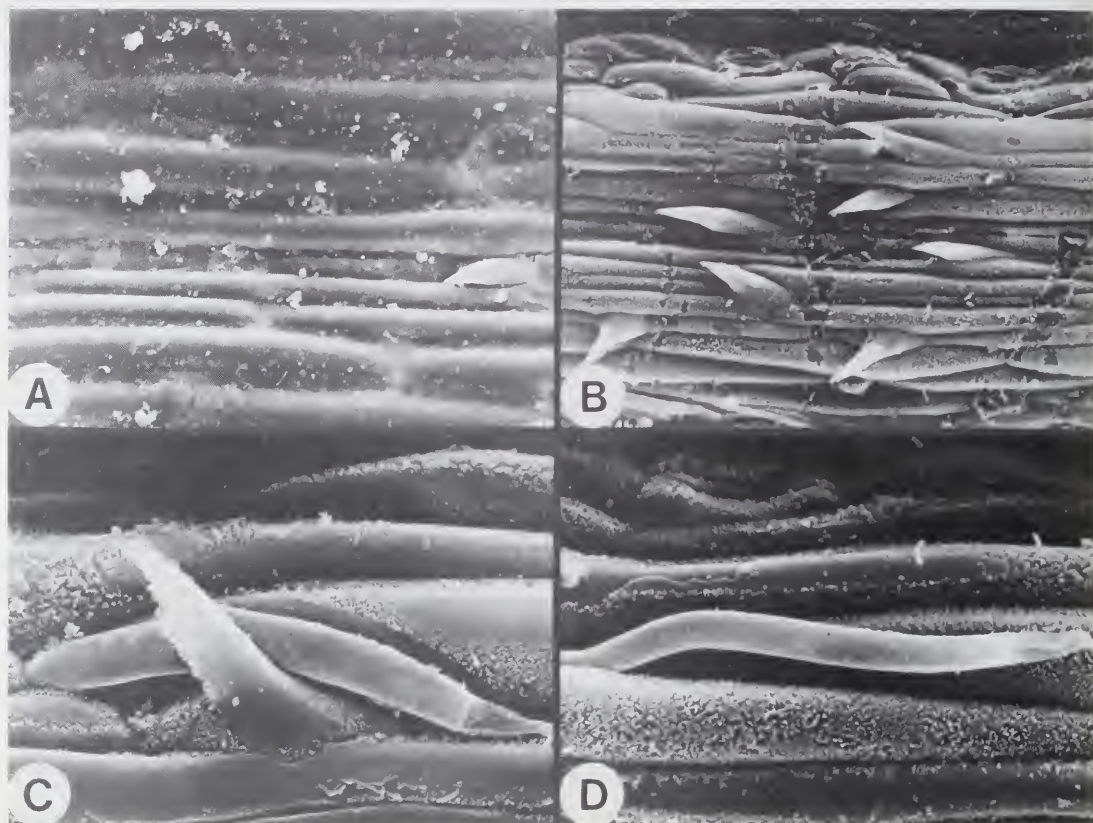


FIGURE 25.2.—*Pentaschistis ampla*: epidermal ultrastructure.

A, featureless abaxial epidermis except for single small prickly cell.

B, adaxial epidermis with prickles on costal ribs and stomata in furrows.

C, adaxial prickly cell and microhair; note short distal cell.

D, narrow, elongate adaxial microhair with minute distal cell in relation to overall hair length.

A–D, *Ellis 5591*. A, B, $\times 200$; D, $\times 550$; C, $\times 650$.

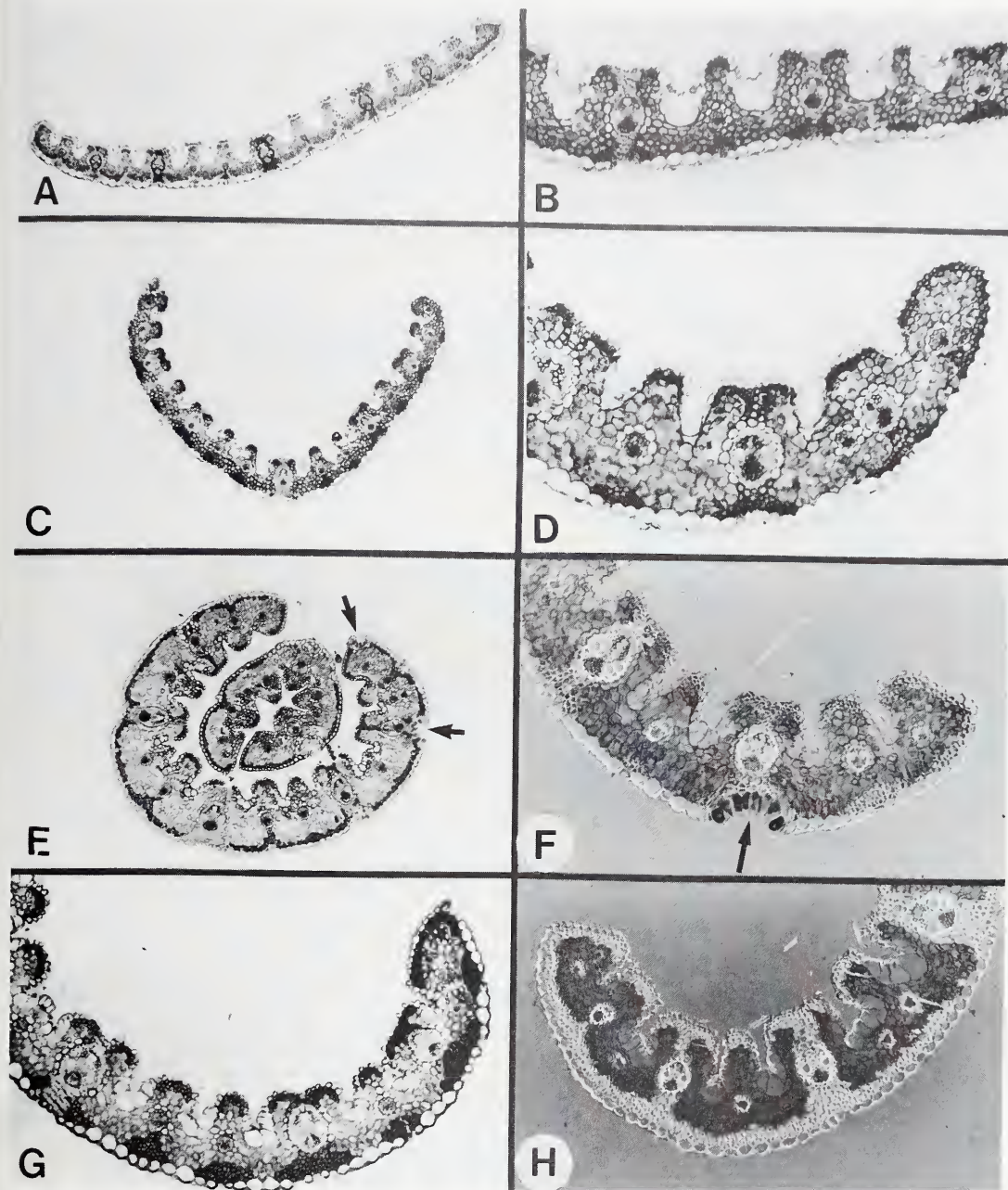


FIGURE 26.1.—*Pentaschistis glandulosa*: leaf blade transverse sections showing variation in the presence of crateriform sunken glands.

- A, open, expanded leaf blade with undifferentiated midrib and no sunken glands.
 B, detail of expanded blade showing ribs and furrows, bulliform cells, mesophyll and sclerenchyma girders.
 C, infolded leaf outline; note lignification of fibres associated with the median vascular bundle and absence of glands.
 D, detail of truncated margin with continuous sclerenchyma layer, diffuse mesophyll and adaxial ribs and furrows.
 E, inrolled blade enfolding young leaf; note presence of sunken glands on both leaves (arrowed).
 F, detail of sunken gland with densely stained gland cells (arrowed); interference contrast.
 G, eglandular leaf anatomy with abaxial sclerenchyma girders almost fused laterally.
 H, eglandular specimen in which the abaxial sclerenchyma forms a continuous hypodermal layer.

A, *Ellis* 2569; B, *Ellis* 5840; C, *Ellis* 5839; D, *Ellis* 5829; E, *Ellis* 5630; F, *Ellis* 629; G, *Ellis* 5609; H, *Ellis* 1653.

A, C, E, $\times 100$; B, D, F–H, $\times 250$.

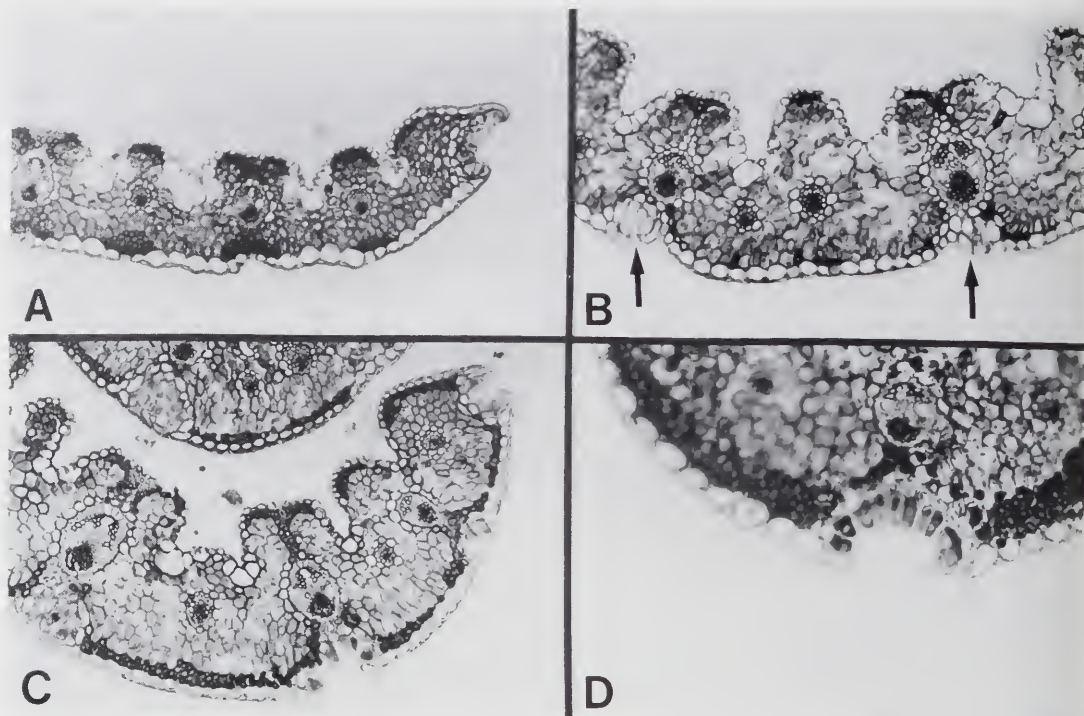


FIGURE 26.2.—*Pentaschistis glandulosa*: anatomical detail of crateriform sunken glands.

A, sunken gland in leaf margin.

B, sunken glands (arrowed) adjacent to the first order vascular bundles.

C, numerous sunken glands in mature as well as unexpanded leaf blades.

D, detail of gland and collar cells of sunken crateriform gland.

A, Ellis 5839; B, Ellis 5631; C, Ellis 5630; D, Ellis 5808; A–C, $\times 250$; D, $\times 400$.

FIGURE 26.3.—*Pentaschistis glandulosa*: abaxial epidermis showing variation in the occurrence of sunken leaf glands.

A, epidermal zonation with costal zones with prickles and intercostal zones without stomata.

B, more detail of intercostal long cells and prickles.

C, distinct costal and intercostal zones; note microhairs (arrowed) but absence of stomata.

D, epidermis of eglandular specimen with continuous hypodermal fibre layer.

E, glands, prickles, microhairs and macrohairs present but no stomata.

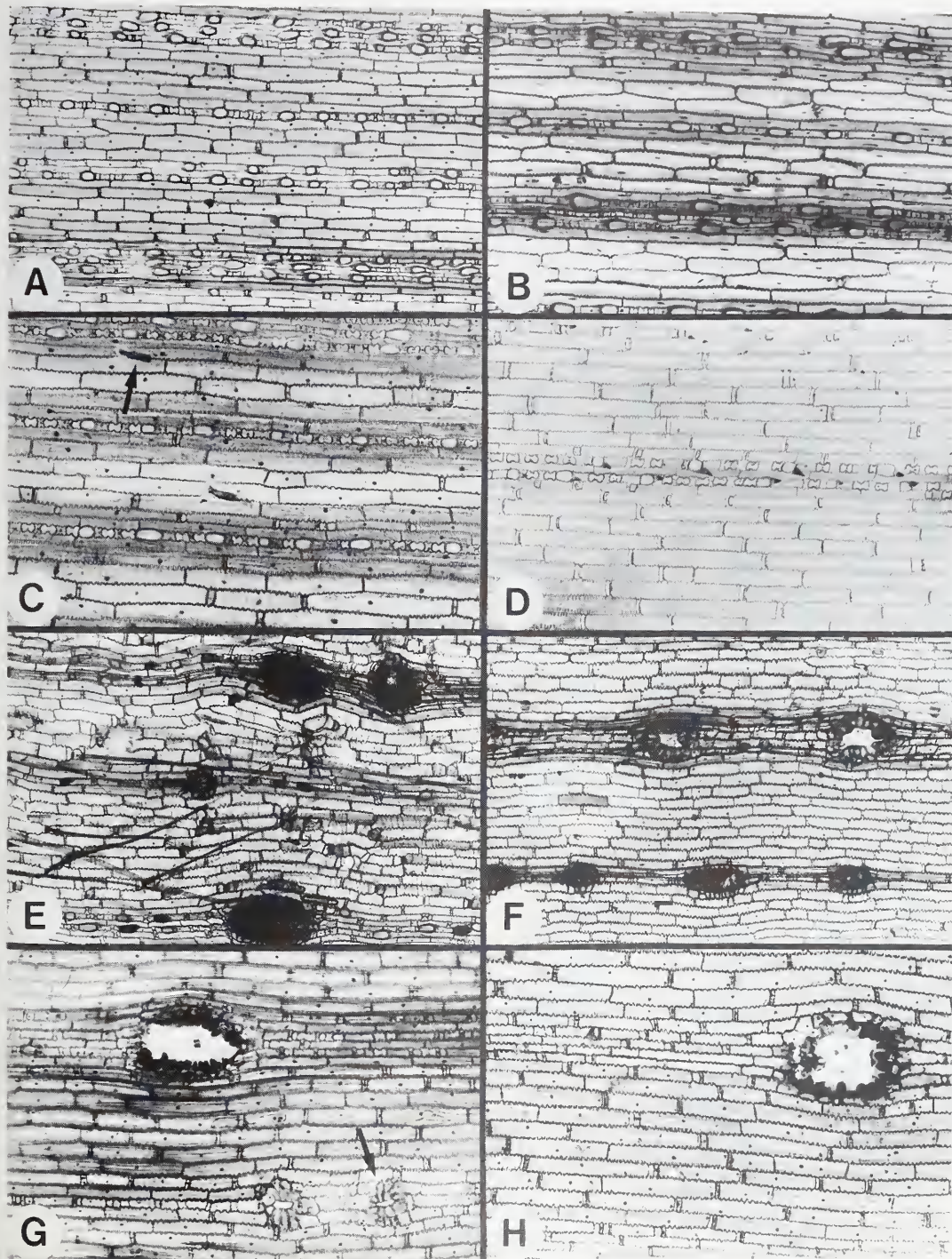
F, rows of glands located in the costal zones with the larger glands subtending the first order bundles and the smaller glands adjacent to the smaller bundles.

G, detail of larger gland with densely staining collar cells and indistinct, sunken, isodiametric gland cells; note very small glands overlying the smaller bundles (arrowed).

H, detail of sunken gland in leaf with continuous hypodermal sclerenchyma layer.

A, Ellis 5829; B, Ellis 5838; C, Ellis 5609; D, Ellis 1653; E, Ellis 5817; F, Ellis 5631; G, Ellis 5630; H, Ellis 5808.

A, E, F, $\times 160$; B–D, G, H, $\times 250$.



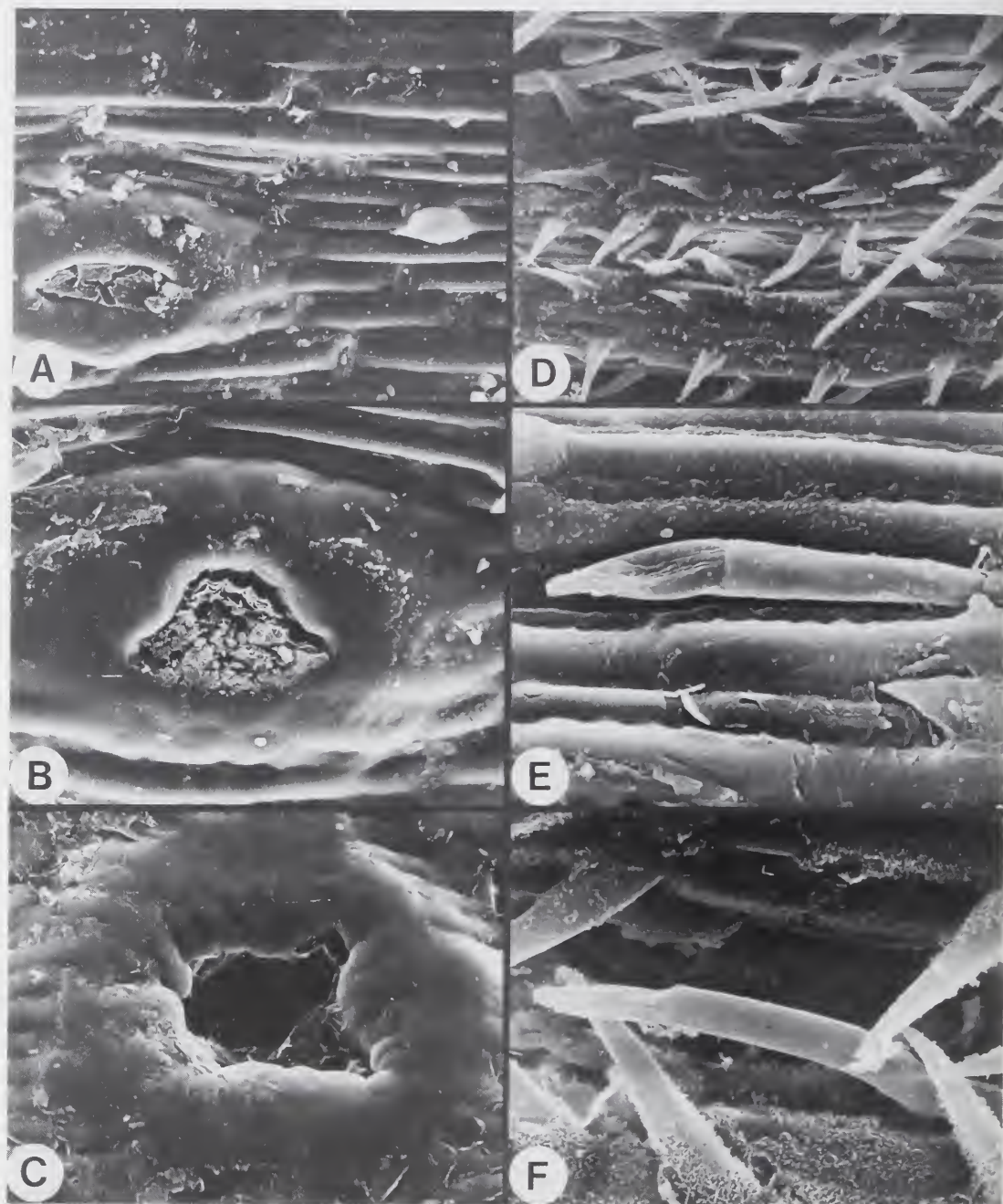


FIGURE 26.4.—*Pentaschistis glandulosa*: epidermal ultrastructure. A–C, abaxial epidermis. D–F, adaxial epidermis. A, epidermal pattern with sunken gland and prickly hair; note absence of stomata. B, detail of crateriform gland with collar cells overarched the crypt in which the gland cells lie. C, further detail of gland crypt and collar cells. D, adaxial epidermis with numerous elongated prickly hairs as well as macrohairs. E, microhair with short, tapering distal cell. F, microhair with short distal cell located amongst prickly hairs. A, B, *Ellis 5808*; C, D, F, *Ellis 5630*, E, *Ellis 5609*. A, D, $\times 200$; B, C, $\times 350$; E, $\times 650$; F, $\times 750$.

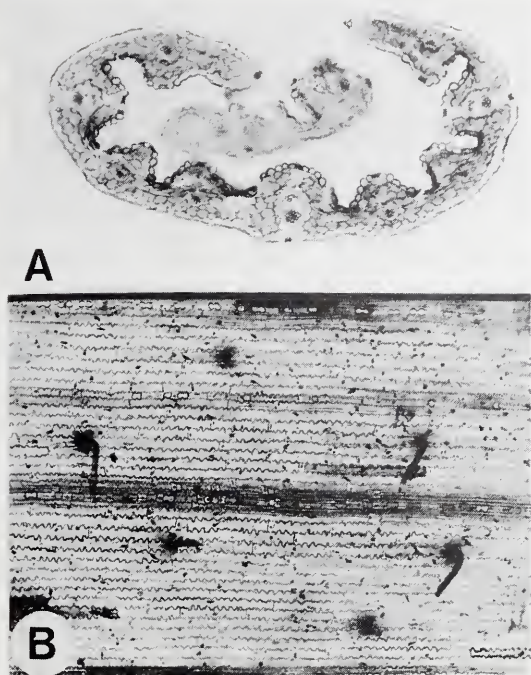


FIGURE 27.1.—*Pentaschistis minor*: leaf blade anatomy. A, very thin, inrolled blade with typical mesic anatomy. B, abaxial epidermis showing zonation, intercostal long cells, absence of stomata and exceptionally long finger-like microhairs. A, Arambourg 188; B, Schlieben 4844. A, B, $\times 250$.

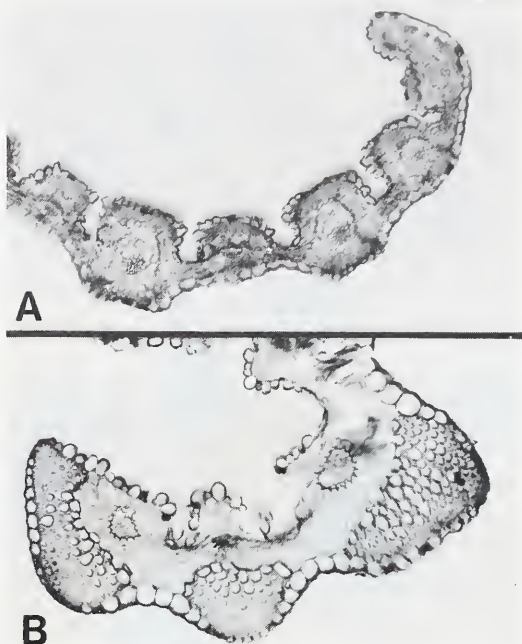


FIGURE 28.1.—*Pentaschistis mannii*: transectional leaf anatomy. A, half of lamina showing reduction in leaf width; adaxial ribs and furrows well developed and all bundles associated with both adaxial and abaxial sclerenchyma girders; no abaxial stomata visible. B, greatly reduced blade containing only 5 vascular bundles; very large abaxial sclerenchyma caps (not linked to the bundle sheaths) form conspicuous 'knees'; no adaxial sclerenchyma present; adaxial epidermal cells inflated papillate. A, Koechlin 7608; B, Meurillon 1198. A, B, $\times 250$.

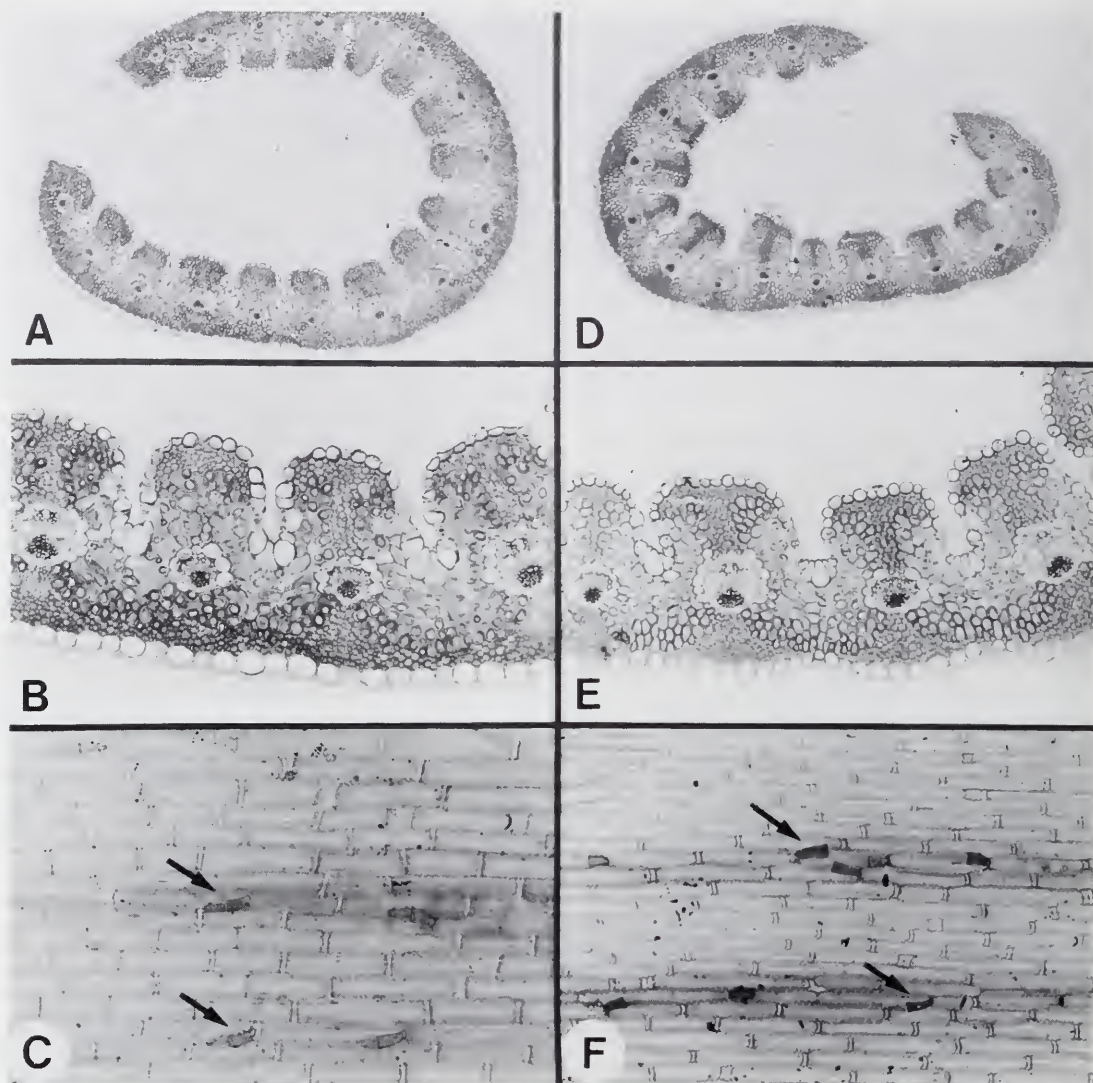


FIGURE 32.1. — *Pentaschistis aristidoides*: specimens with anatomy resembling the sclerophyllous type i.e. relatively compact mesophyll and no abaxial stomata.

A, rather narrow, inrolled leaf outline.

B, detail of adaxial ribs and steep furrows, rather compact chlorenchyma and fused abaxial girders forming continuous subepidermal layer overlying epidermis of very uniform cells.

C, abaxial epidermis without distinguishable costal and intercostal zones, stomata are absent, long cells separated by single tall short cells or silica bodies and microhairs (arrowed) common.

D, inrolled leaf blade.

E, transsectional detail very similar to B.

F, abaxial epidermis showing files of microhairs (arrowed) in the centre of the undifferentiated intercostal zones i.e. directly beneath the adaxial furrows between the vascular bundles, microhairs with basal and distal cells equal in length.

A–C, *Ellis* 2282; D–F, *Ellis* 2283. A, D, $\times 100$; B, C, E, F, $\times 250$.

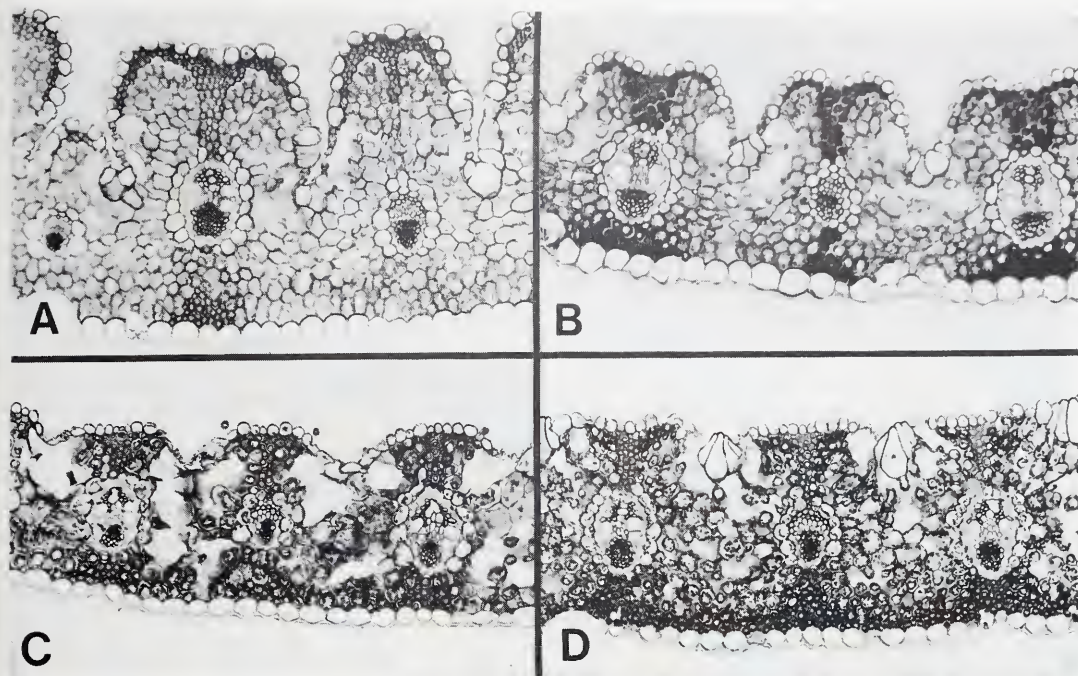
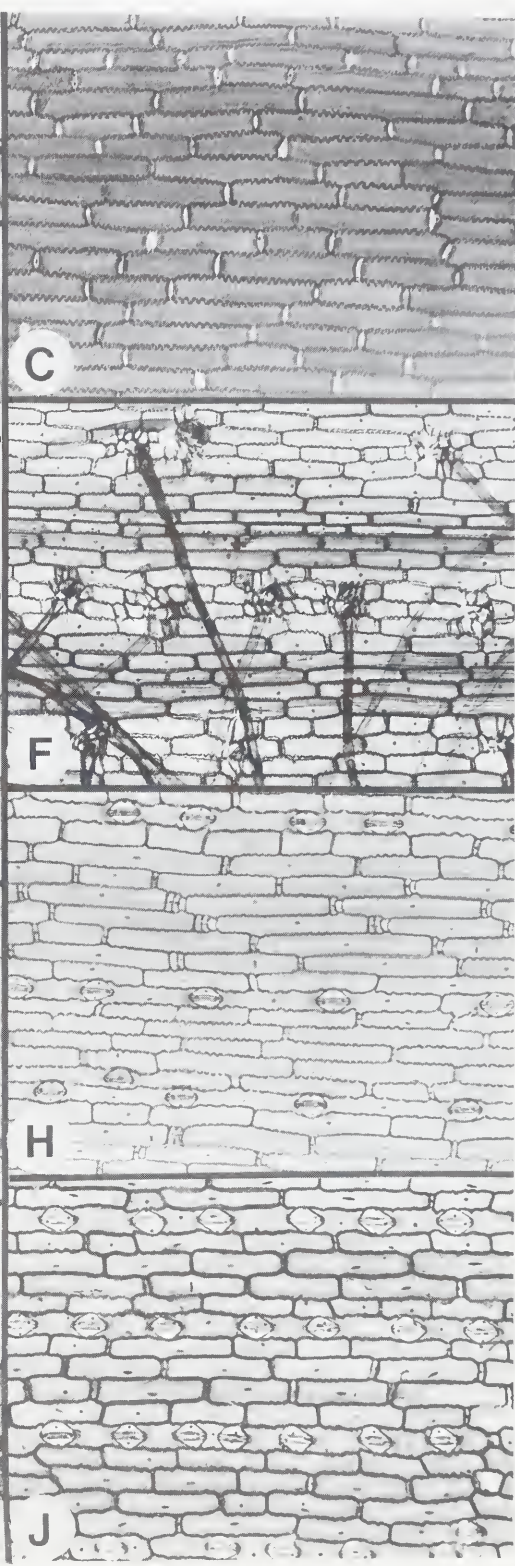
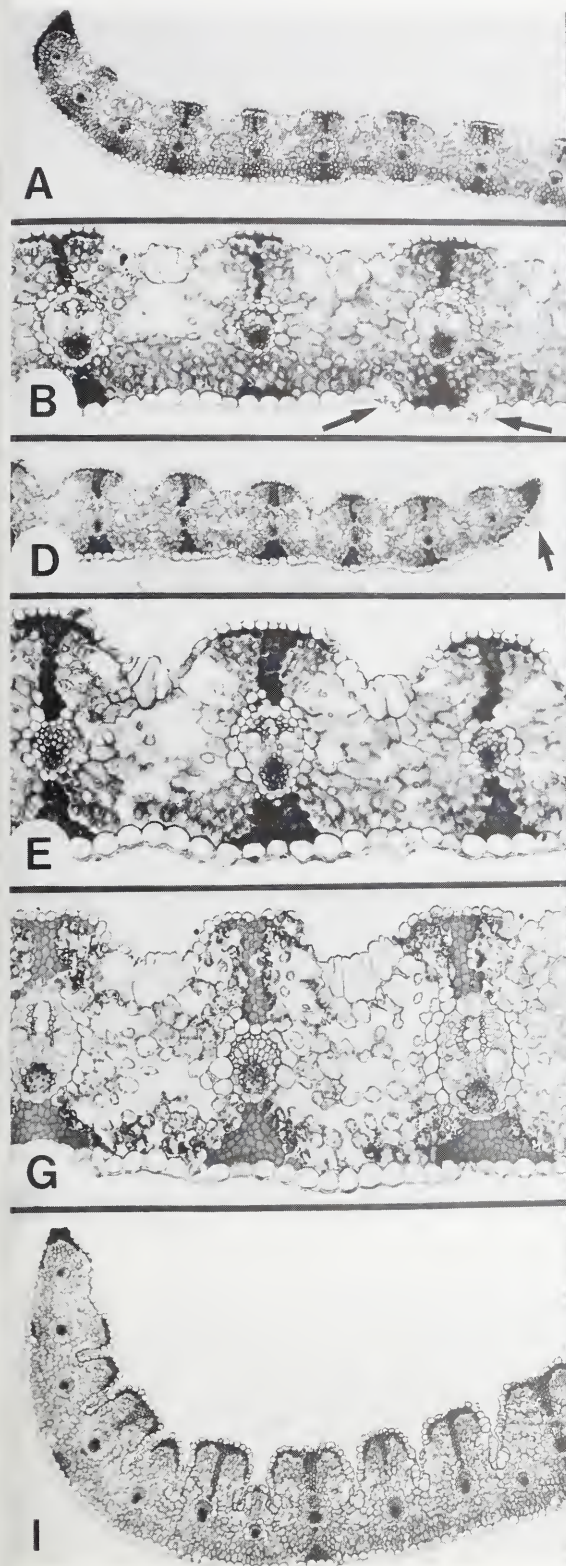


FIGURE 32.2.—*Pentaschistis aristidoides*: variation in adaxial ribs, chlorenchyma and sclerenchyma girders. A, well-developed adaxial ribs with cleft-like furrows, rather compact chlorenchyma with small intercellular air spaces and abaxial girders only in association with the first order vascular bundles. B, adaxial ribs with steep but open furrows, chlorenchyma with large intercellular air spaces near the bases of the furrows and abaxial girders associated with all bundles. C, shallow, wide adaxial furrows, diffuse chlorenchyma of large parenchymatous cells and all vascular bundles linked to both adaxial and abaxial girders. D, ribs and furrows not present, chlorenchyma diffuse and abaxial girders fused to form a continuous hypodermal layer. A, *Ellis* 5566; B, *Ellis* 5440; C, *Ellis* 2504; D, *Ellis* 2487. All $\times 250$.

FIGURE 32.3.—*Pentaschistis aristidoides*: leaf anatomy showing lack of congruence between transectional and epidermal anatomy in specimens lacking a continuous hypodermal sclerenchyma layer as seen in transection. A–C, *Ellis* 5687 with no abaxial stomata or macrohairs. D–F, *Ellis* 5778 with no abaxial stomata but with macrohairs. G, H, *Ellis* 5428 with abaxial stomata but no macrohairs. I, J, *Ellis* 5566 with abaxial stomata but with more compact chlorenchyma.

- A, wide, expanded leaf outline.
 - B, transectional detail showing shallow adaxial furrows, diffuse chlorenchyma and small adaxial and abaxial sclerenchyma girders, stomata (arrowed) are visible in the abaxial epidermis but not in the epidermal preparation.
 - C, abaxial epidermis without discernible zonation, stomata, macrohairs or microhairs; long cells in brickwork pattern, all separated by single tall but narrow silica body.
 - D, expanded, open leaf blade with macrohair cushion base near margin (arrowed).
 - E, transectional detail very similar to B.
 - F, abaxial epidermis with costal and intercostal zones, stomata and microhairs are not present but long, flexible macrohairs with cushion bases occur in the intercostal files.
 - G, transectional anatomy showing shallow adaxial furrows, diffuse chlorenchyma and discrete abaxial sclerenchyma girders.
 - H, abaxial epidermis with stomatal files in intercostal zones; note costal silica bodies which are closely associated with one or two short cells.
 - I, leaf outline with deep adaxial furrows but very few vascular bundles with abaxial girders or strands. Figure 32.3 A illustrates the same leaf under higher magnification.
 - J, files of stomata common, costal and intercostal long cells identical in size and shape but no microhairs.
- A–C, *Ellis* 5787; D–F, *Ellis* 5778; G, H, *Ellis* 5428; I, J, *Ellis* 5566. A, D, I, $\times 100$; B, C, E–H, J, $\times 250$.



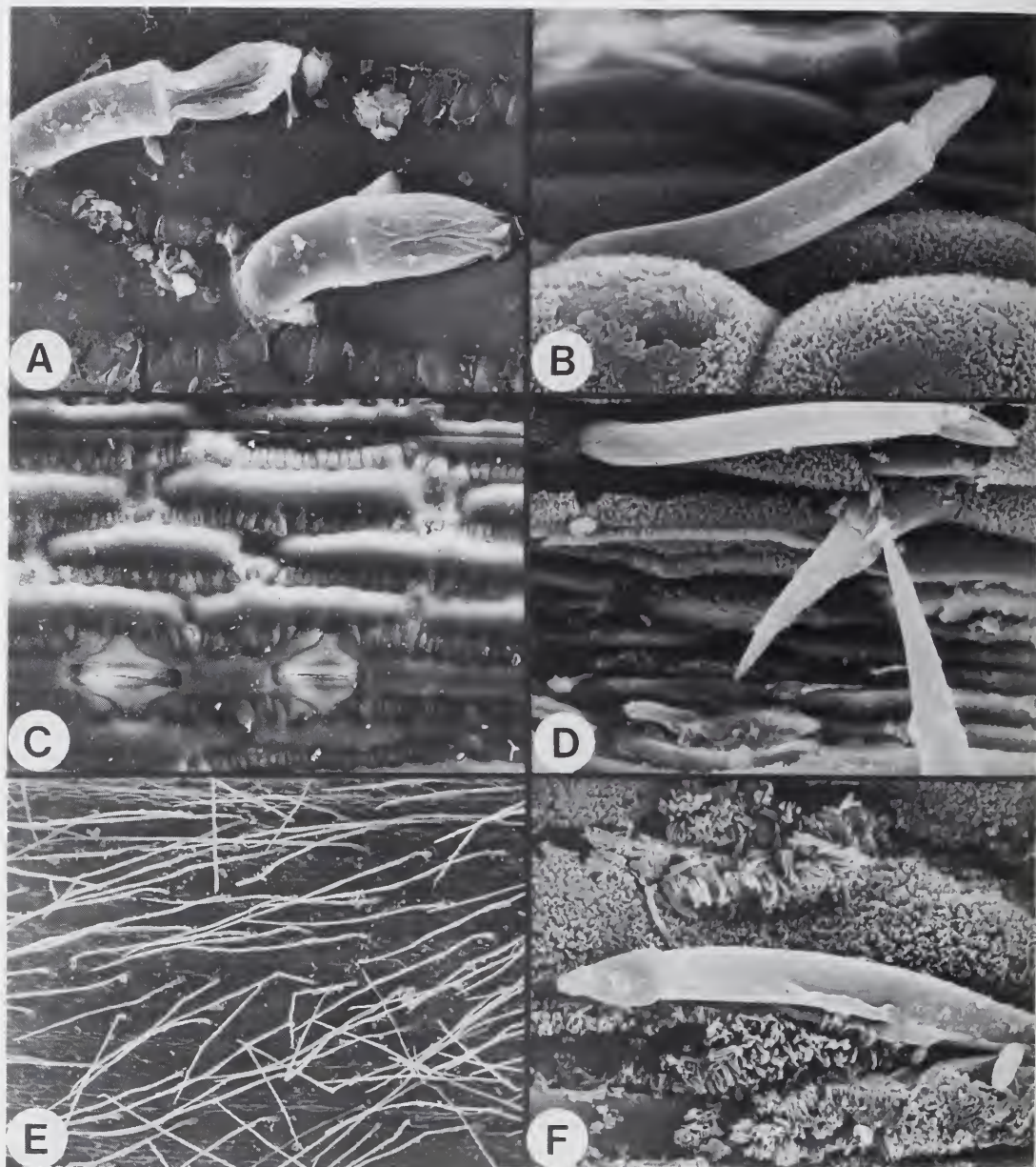


FIGURE 32.4.—*Pentaschistis aristidoides*: leaf epidermal ultrastructure. A, B, abaxial and adaxial microhairs. C, D, abaxial and adaxial epidermal cells. E, F, lower and upper leaf surface.

A, short, broad abaxial microhair with distal and basal cells of equal length.

B, elongated, finger-like adaxial microhair with very short distal cell.

C, abaxial epidermis with thick-walled, sinuous-long cells and stomata with triangular subsidiary cells and no microhairs.

D, adaxial epidermis with elongated, inflated long cells, prickles and finger-like microhair with short distal cell.

E, abaxial epidermis with dense indumentum of long, flexible macrohairs.

F, adaxial epidermis showing thick layer of epicuticular wax and elongated microhair with small distal cell.

A, B, *Ellis 5566*; C, D, *Ellis 5440*; E, F, *Ellis 5778*. A, $\times 600$; B, F, $\times 650$; C, $\times 200$; D, $\times 450$; E, $\times 20$.

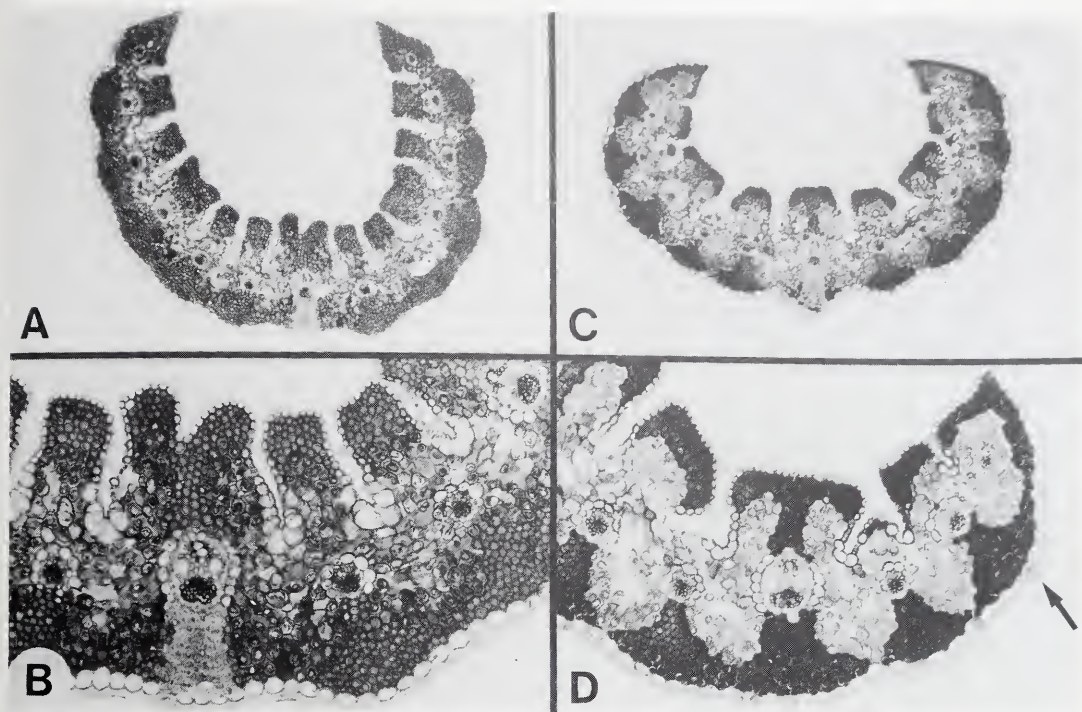


FIGURE 33.1.—*Pentaschistis velutina*: transectional anatomy.

A, inrolled leaf outline showing thick blade with sharply tapering margins.

B, detail of midrib region with massive, flat-topped ribs, cleft-like furrows, rather diffuse chlorenchyma and well-developed adaxial strands (3'vbs) or girders (1'vbs) and fused abaxial girders.

C, diagnostic leaf outline.

D, detail of leaf margin with darkly staining sclerenchyma tissue and gland-like cell in section (arrowed).

A, B, *Ellis* 2490; C, *Ellis* 5799; D, *Ellis* 5798. A, C, $\times 100$; B, D, $\times 250$.

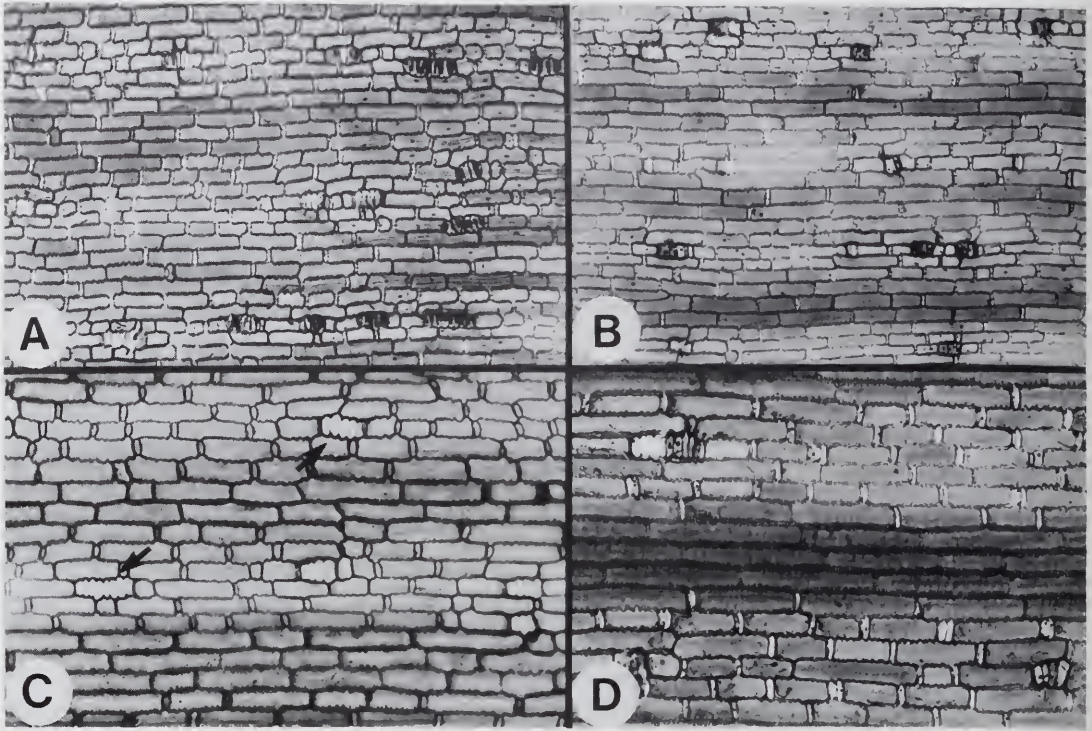


FIGURE 33.2.—*Pentaschistis velutina*: abaxial epidermis.

- A, epidermal pattern showing absence of zonation and stomata; note short files of gland-like cells, often with darkly staining contents.
 B, no zonation or stomata present but short, sessile, linear glands conspicuous.
 C, epidermal detail with slightly elongated long cells with thickened walls separated in a file by single, tall and narrow short cells; scattered throughout the epidermis are translucent, short, sessile linear glands (arrowed).
 D, epidermal detail of thick, sinuous, long cell walls and sessile linear glands.
- A, *Ellis 5512*; B, *Ellis 5798*; C, *Ellis 2490*; D, *Ellis 5799*. A, B, $\times 160$; C, D, $\times 250$.

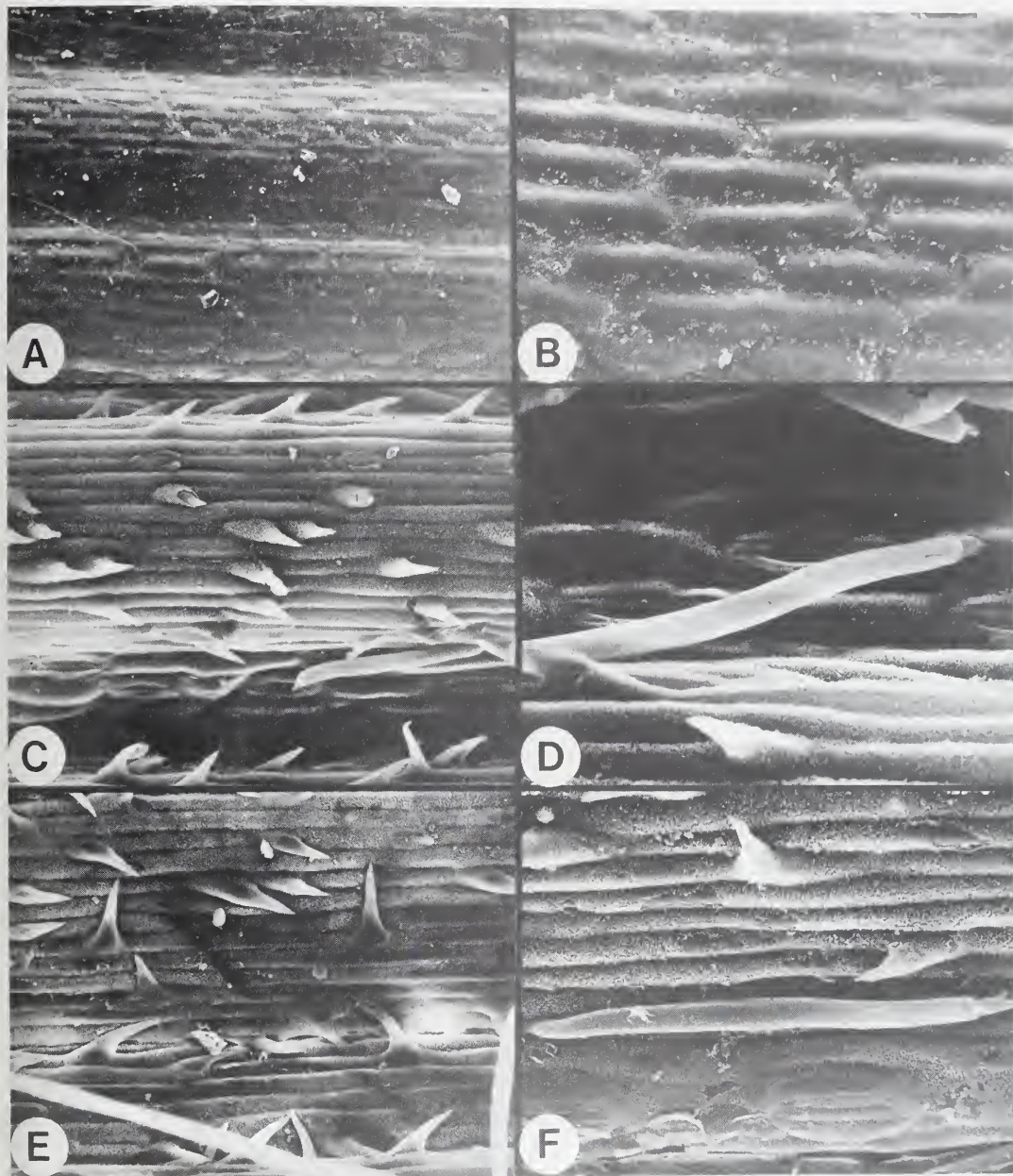


FIGURE 33.3.—*Pentaschistis velutina*: scanning electron microscopy of both epidermides. A, B, abaxial epidermis.

C–F, adaxial epidermis.

A, raised costal zones but otherwise this surface featureless.

B, inflated periclinal long cell walls and thickened, sinuous anticlinal walls; no stomata or epidermal appendages and linear glands not visible with SEM.

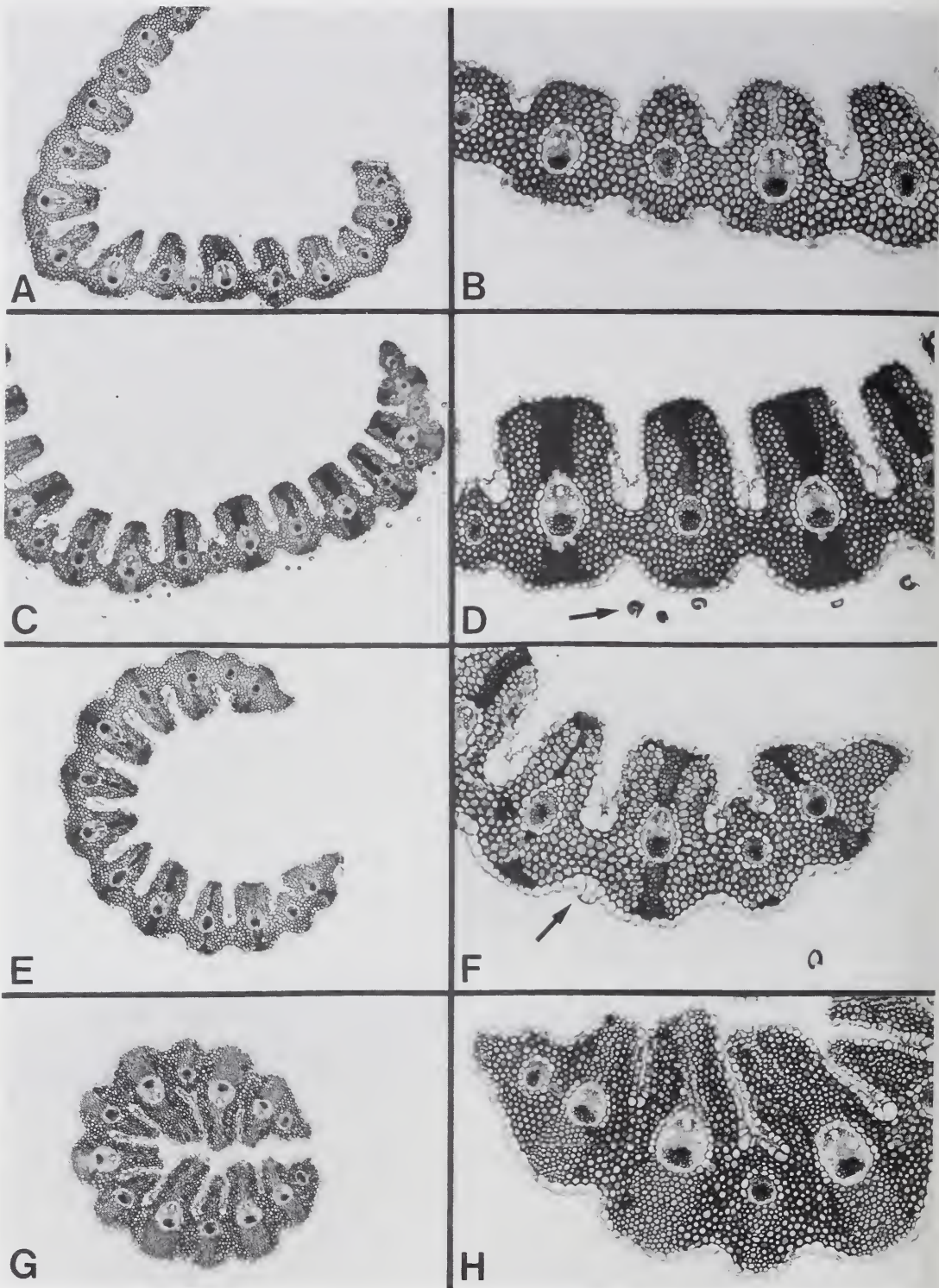
C, small prickles on costal ribs with narrow, elongated costal long cells.

D, very elongated, narrow microhair with very short and small distal cell.

E, elongate, narrow costal long cells, prickles with short barbs and part of superficial macrohair.

F, detail of prickles, stoma and very long microhair with minute distal cell.

A, C, D, *Ellis* 5799; B, E, F, *Ellis* 4630. A, $\times 60$; B, C, E, $\times 200$; D, $\times 450$; F, $\times 400$.



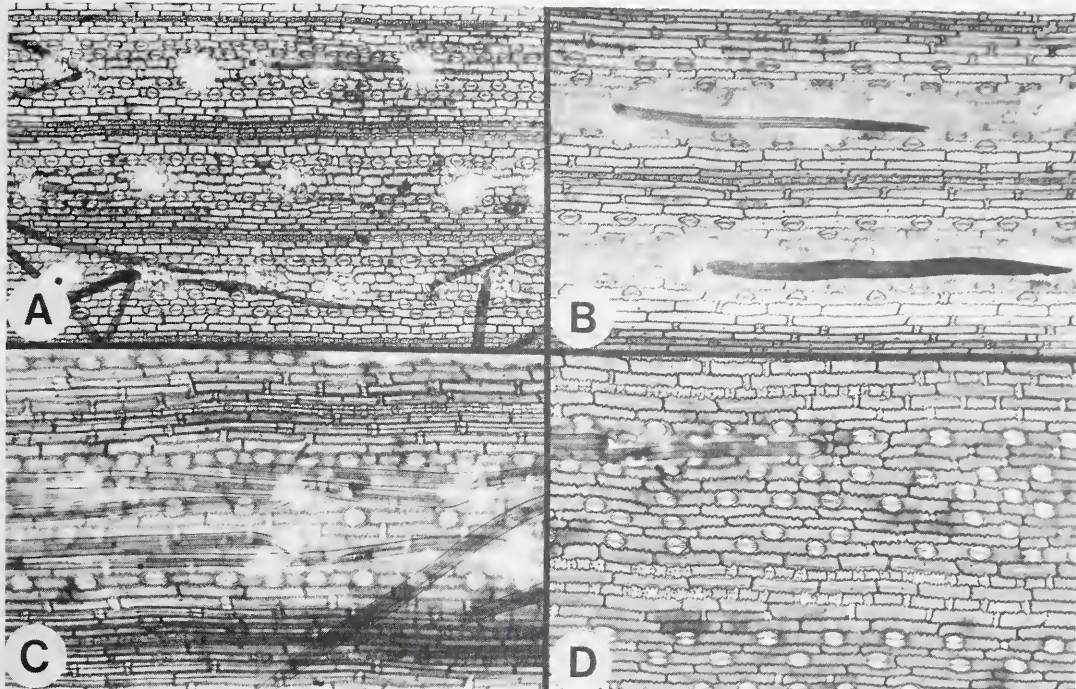


FIGURE 34.2.—*Pentaschistis viscidula*: abaxial epidermis.

- A, epidermal zonation showing costal zones with silica bodies and intercostal zones with stomata and macrohairs.
 B, two stiff, thick-walled, superficial macrohairs lying along the abaxial furrows or intercostal zones; note only a few specialized epidermal cells associated with the constricted bases of these hairs.
 C, many macrohairs overlying the stomata of the intercostal zones.
 D, costal zones with tall and narrow silica bodies, intercostal zones with stomatal files and macrohairs.
 A, *Ellis* 5558; B, *Ellis* 5488; C, *Ellis* 5492; D, *Ellis* 5529. A, $\times 160$; B–D, $\times 250$.

FIGURE 34.1.—*Pentaschistis viscidula*: transectional leaf anatomy.

- A, relatively broad but infolded outline with undifferentiated midrib; note moniliform outline with adaxial and abaxial ribs.
 B, adaxial ribs and furrows but shallow abaxial furrows and slight ribs; chlorenchyma of compact small isodiametric cells.
 C, broad leaf transection with slight inrolling and sectioned macrohairs visible below the abaxial epidermis.
 D, detail of abaxial and adaxial ribs and furrows, sclerenchyma girders without lignified secondary walls and compact chlorenchyma; note abaxial macrohairs in section (arrowed).
 E, narrow, inrolled leaf blade.
 F, detail of lateral part of lamina showing adaxial and abaxial ribs and furrows and base of macrohair (arrowed) with few raised cushion cells in base of abaxial furrow.
 G, strongly inrolled, setaceous outline.
 H, ribs and furrows on both surfaces, chlorenchyma of compact, isodiametric cells and sclerenchyma girders not lignified.
 A, B, *Ellis* 5489; C, D, *Ellis* 5492; E, F, *Ellis* 5558; G, H, *Ellis* 5529. A, C, E, G, $\times 100$; B, D, F, H, $\times 250$.

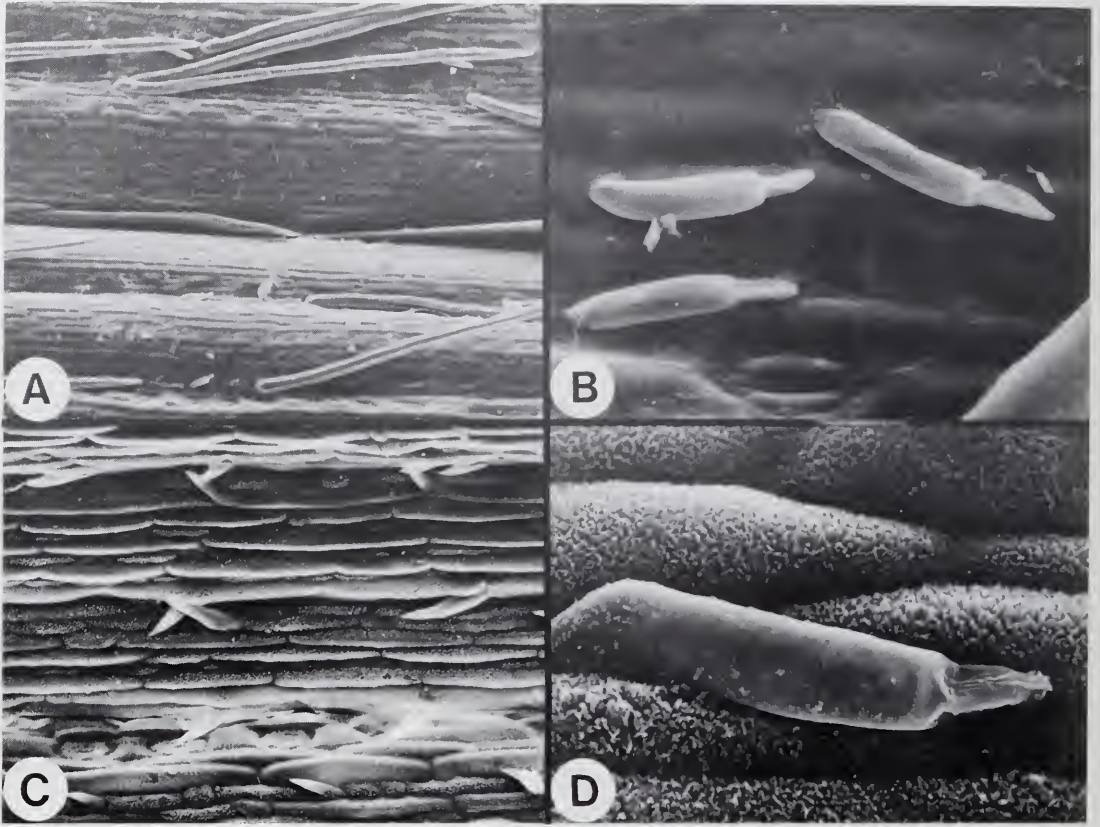


FIGURE 34.3.—*Pentaschistis viscidula*: epidermal ultrastructure. A, B, abaxial epidermis. C, D, adaxial epidermis. A, rigid macrohairs located in abaxial furrows between ribs. B, microhairs with basal cells at least twice as long as the distal cells; note stoma flush with epidermal surface. C, inflated but elongated intercostal and costal long cells overarching stomata; note small hooks. D, rare adaxial microhair with distal cell relatively much shorter than those of the abaxial surface in B. A, B, *Ellis 5529*; C, *Ellis 5488*; D, *Ellis 5492*. A, $\times 50$; B, $\times 500$; C, $\times 200$; D, $\times 1350$.

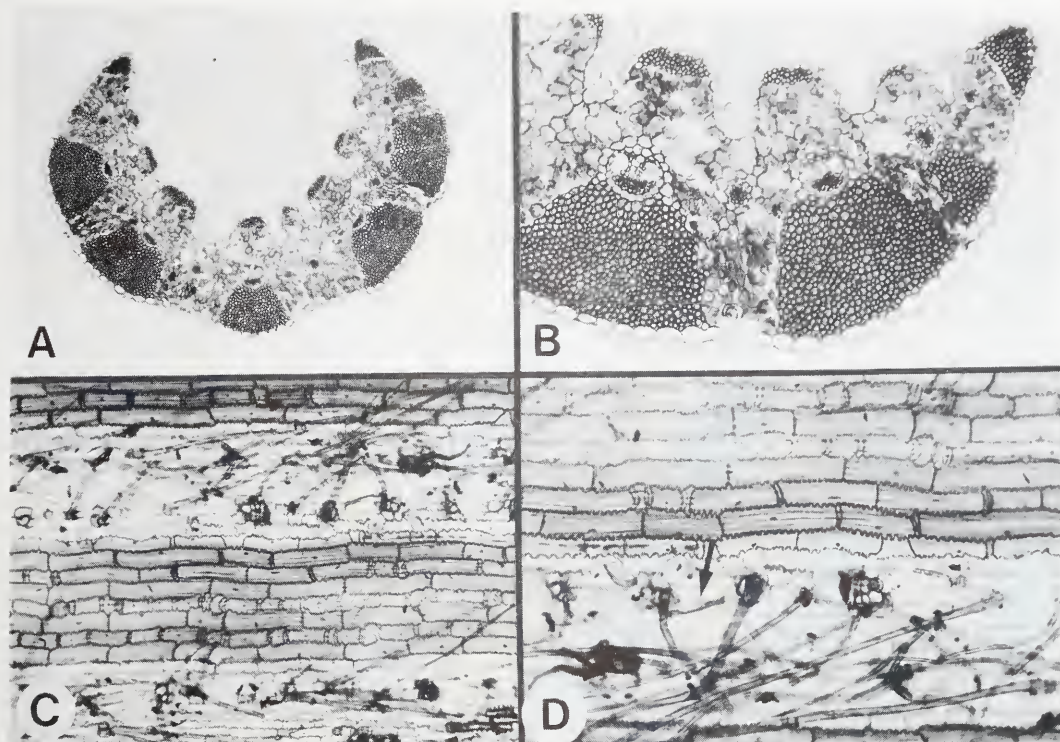


FIGURE 34.4.—*Pentaschistis viscidula*: specimen which differs substantially from the rest of the specimens assigned to this taxon and may represent a new species. A, B, leaf in transverse section. C, D, abaxial epidermis. A, narrow, inrolled leaf blade outline with unusual disposition of sclerenchyma girders. B, detail of lateral part of leaf blade showing massive abaxial girders associated with first order bundles only and diffuse nature of the chlorenchyma. C, epidermal zonation with broad costal zones of short, but wide, long cells and few tall silica bodies; intercostal zones with narrower long cells, stomata and soft, flexible macrohairs. D, detail of costal long cells and silica bodies and intercostal stomata and macrohairs with cushion bases of 5–7 cells; note very thin and elongated basal cell of microhair (arrowed). A–D, *Ellis* 5589. A, $\times 100$; C, $\times 160$; B, D, $\times 250$.

FIGURE 35.1.—*Pentaschistis argentea*: transectional leaf anatomy.

A, broadly V-shaped leaf outline.

B, slight adaxial ribs and furrows with well-developed bulliform cells at bases of furrows; chlorenchyma cells compact.

C, wide but infolded blade outline.

D, no adaxial ribs and furrows present in lateral parts of lamina; chlorenchyma of small, tightly packed, isodiametric cells with very small intercellular air spaces; 1'vbs alternate with 3'vbs; abaxial and adaxial epidermal cells of similar size.

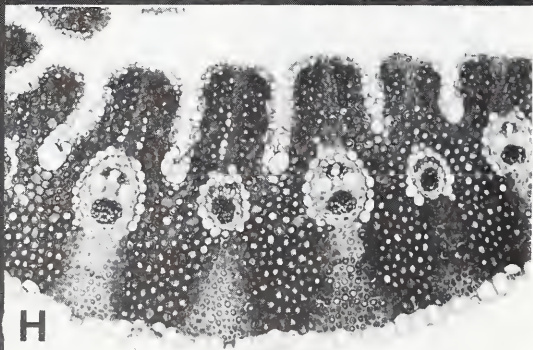
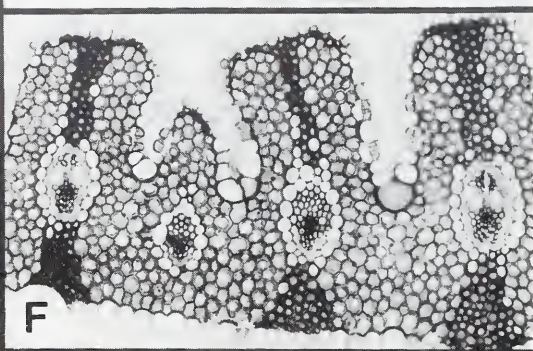
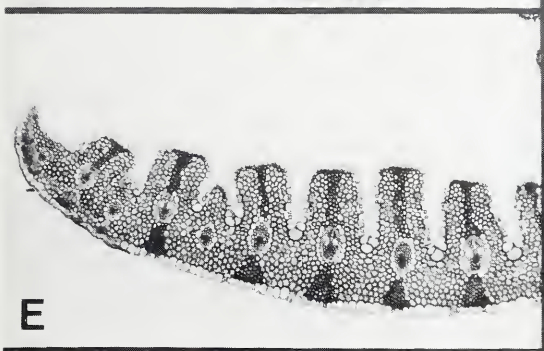
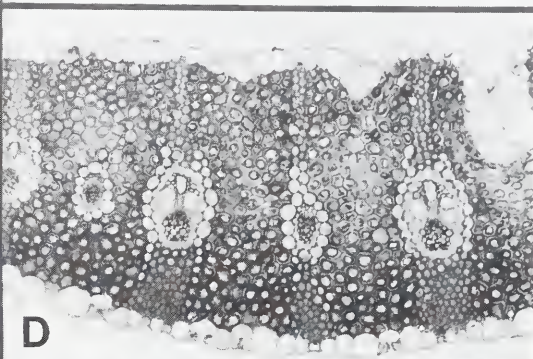
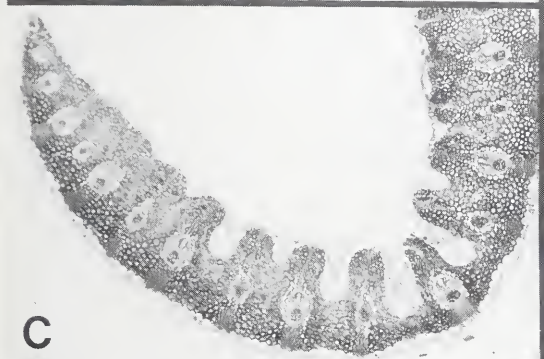
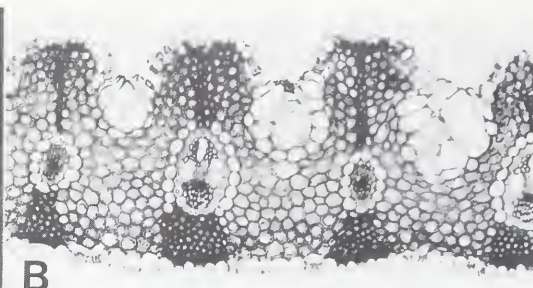
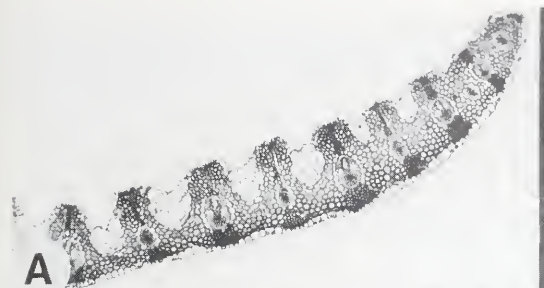
E, one half of V-shaped lamina outline.

F, cleft-like adaxial furrows with very small bulliform cells at their bases; well-developed ribs with inversely anchor-shaped sclerenchyma girders with cellulose secondary walls; compact mesophyll.

G, permanently infolded acicular leaf blade.

H, adaxial ribs, cleft-like furrows and small bulliform cells; compact mesophyll of small isodiametric cells; massive, trapezoidal abaxial girders and T-shaped adaxial girders; fibres with cellulose thickening—only mestome sheath lignified.

A, B, *Ellis* 5552; C, D, *Ellis* 2542; E, F, *Ellis* 5561; G, H, *Ellis* 2284. A, C, E, G, $\times 100$; B, D, F, H, $\times 250$.



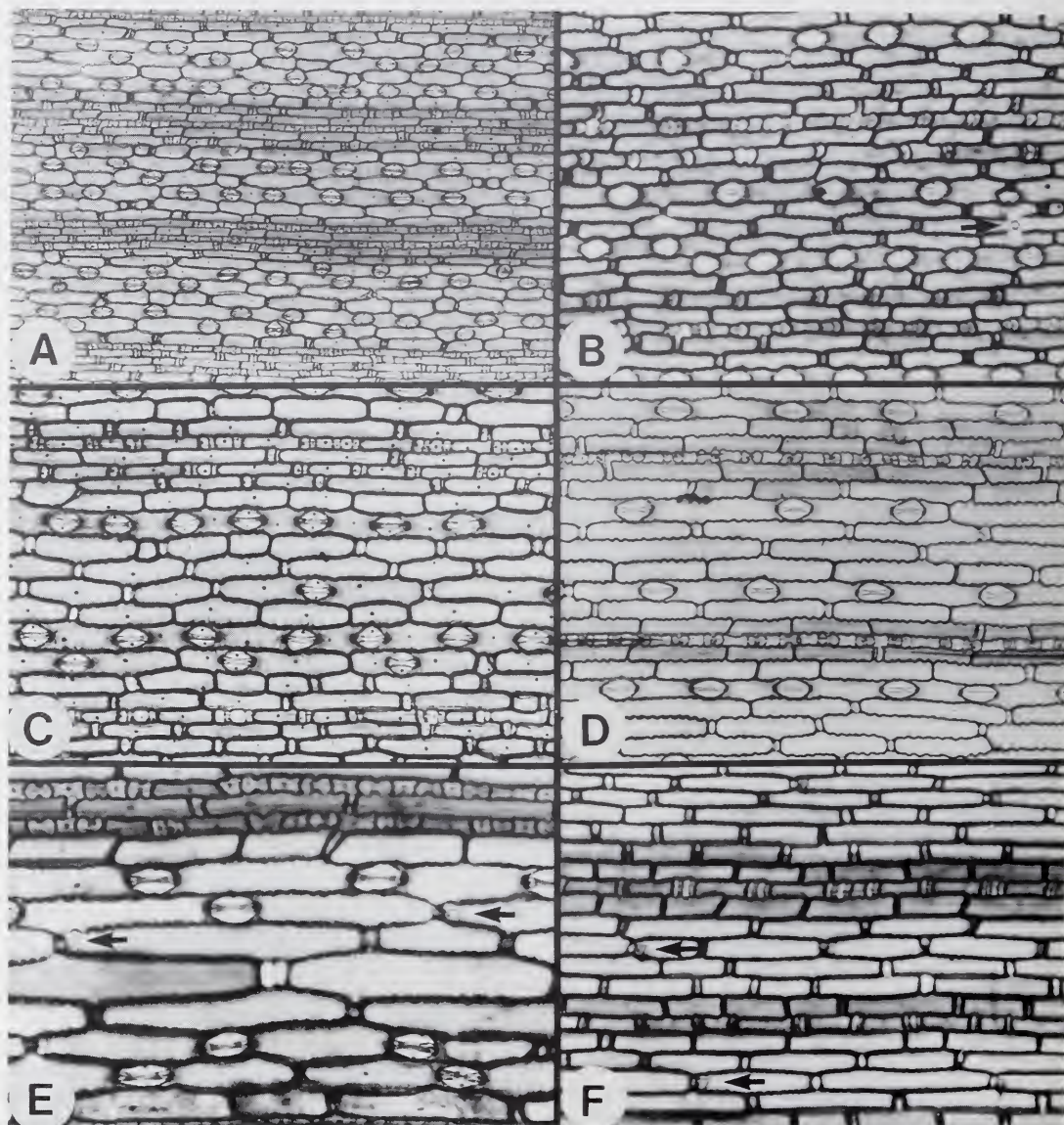


FIGURE 35.2.—*Pentaschistis argentea*: abaxial epidermis.

- A, epidermal zonation evident with costal zones with silica bodies and intercostal zones with files of stomata.
 B, costal zones with irregular silica bodies closely associated with cork cells and intercostal zones with files of low dome-shaped stomata; basal cells of microhairs (arrowed) visible in intercostal zones.
 C, intercostal zone between two costal zones of narrower cells in which silica bodies are irregularly located, either as pairs or short files of cork-silica cells; files of stomata and short, fusiform long cells separated by single silica cells comprise the intercostal zone.
 D, stomatal files with stomata separated by single interstomatal cell; long cells elongated, slightly fusiform with slightly sinuous walls; costal zones only three cells wide with central file with irregularly dumbbell-shaped silica bodies.
 E, detail of epidermal cells—stomata, fusiform long cells, intercostal short cells separating long cells and basal cells of microhairs (arrowed); irregularly dumbbell-shaped silica bodies in costal zone.
 F, unusual specimen with very few abaxial stomata and with costal and intercostal zones evident; note microhairs (arrowed).

A, *Ellis 5552*; B, *Ellis 5493*; C, *Ellis 5561*; D, *Ellis 2291*; E, *Ellis 5154*; F, *Ellis 5494*. A, $\times 160$; B–D, F, $\times 250$; E, $\times 400$.

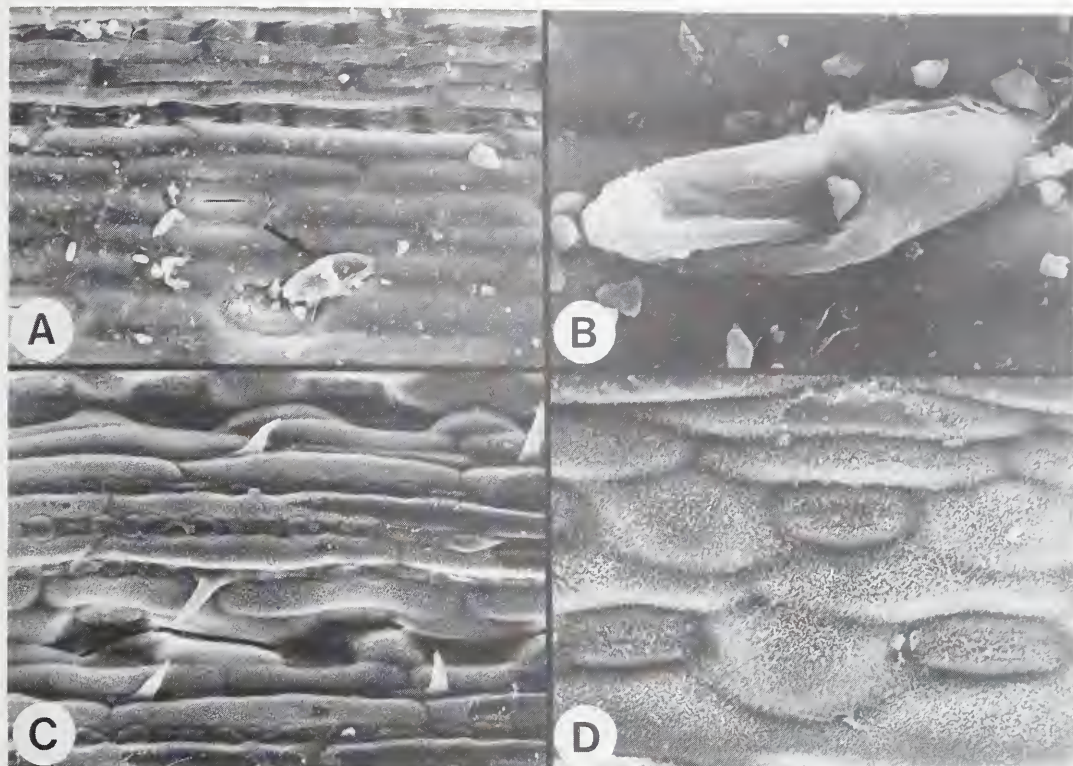


FIGURE 35.3.—*Pentaschistis argentea*: epidermal ultrastructure. A, B, abaxial epidermis. C, D, adaxial epidermis.

A, costal zone with silica bodies in top half of picture; stomatal pore and microhair (arrowed) in intercostal zone in lower half of micrograph.

B, short, broad abaxial microhair with distal cell slightly longer than basal cell.

C, central costal zone with dumbbell-shaped to nodular silica bodies, inflated intercostal long cells and small hooks; no microhairs observed.

D, detail of intercostal long cells with inflated anticlinal walls overarchng stomata and epicuticular wax.

A, *Ellis 5493*; B, C, *Ellis 5541*; D, *Ellis 5154*. A, C, $\times 200$; D, $\times 400$; B, $\times 1000$.

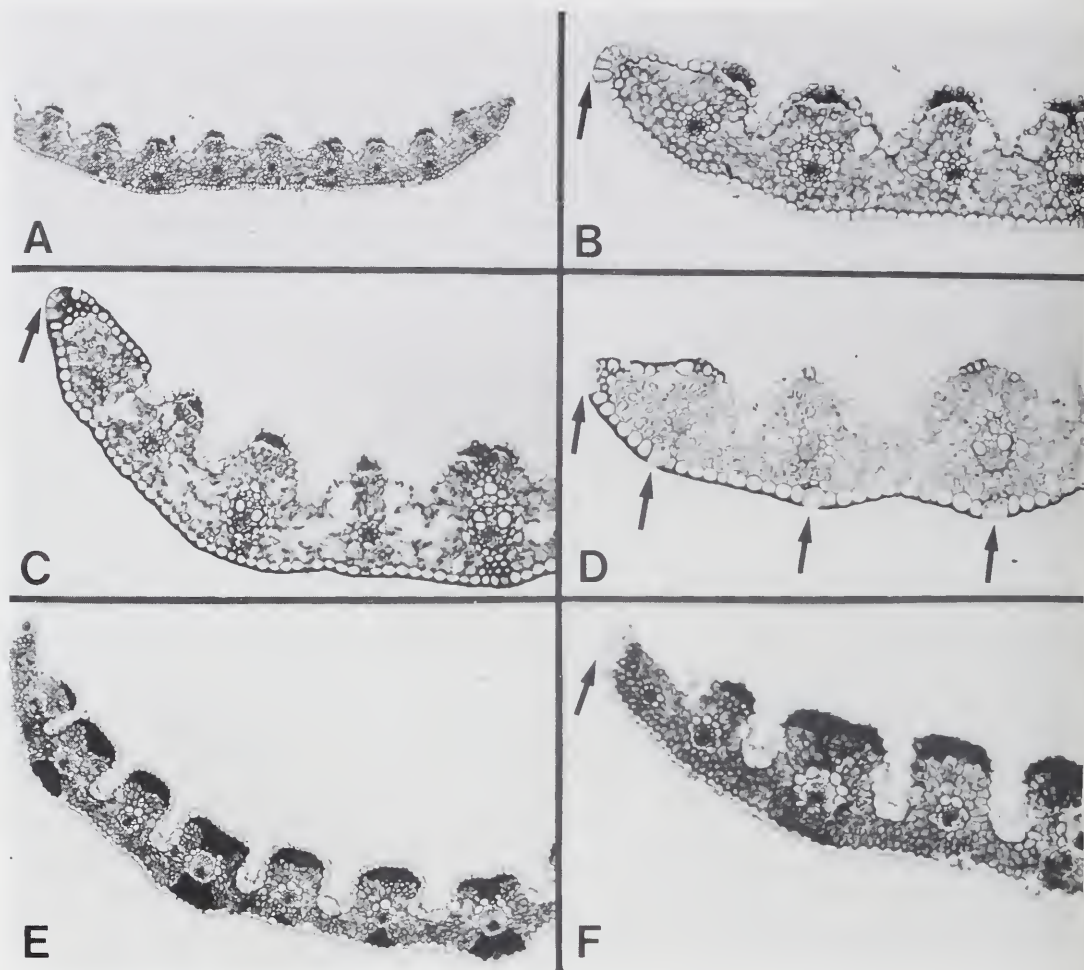


FIGURE 36.1.—*Pentaschistis trisetata*: leaf blade transections showing location of linear glands in slightly tapering margins. A–D, specimens with soft, mesic anatomy collected in first year after fire. E, F, specimen with well-developed supporting tissue collected in second post-fire season at same locality as A, B and C.

A, expanded leaf outline with median vascular bundle structurally identical to lateral first order bundles.

B, leaf margin with linear gland cells (arrowed); note absence of chloroplasts in outer bundle sheath cells.

C, tapering leaf margin with linear gland cells in section (arrowed).

D, lateral part of leaf blade showing triseriate marginal linear gland as well as uni- or biseriate linear glands in the abaxial costal zones (arrowed).

E, slightly inrolled outline of strengthened leaf with deep adaxial furrows and pronounced ribs, dense chlorenchyma, well-developed sclerenchyma girders and margin a tapering projection; compare with anatomy of *P. rosea* subsp. *purpurascens* (Figure 37b.1).

F, detail of projecting margin with linear gland cells (arrowed); note compact chlorenchyma, sclerenchyma girders associated with the first order vascular bundles, the adaxial ribs and furrows and the very thick abaxial cuticle.

A, B, *Ellis* 5422; C, *Ellis* 5421; D, *Ellis* 5429; E, F, *Ellis* 5783. A, $\times 100$; E, $\times 160$; B–D, F, $\times 250$.

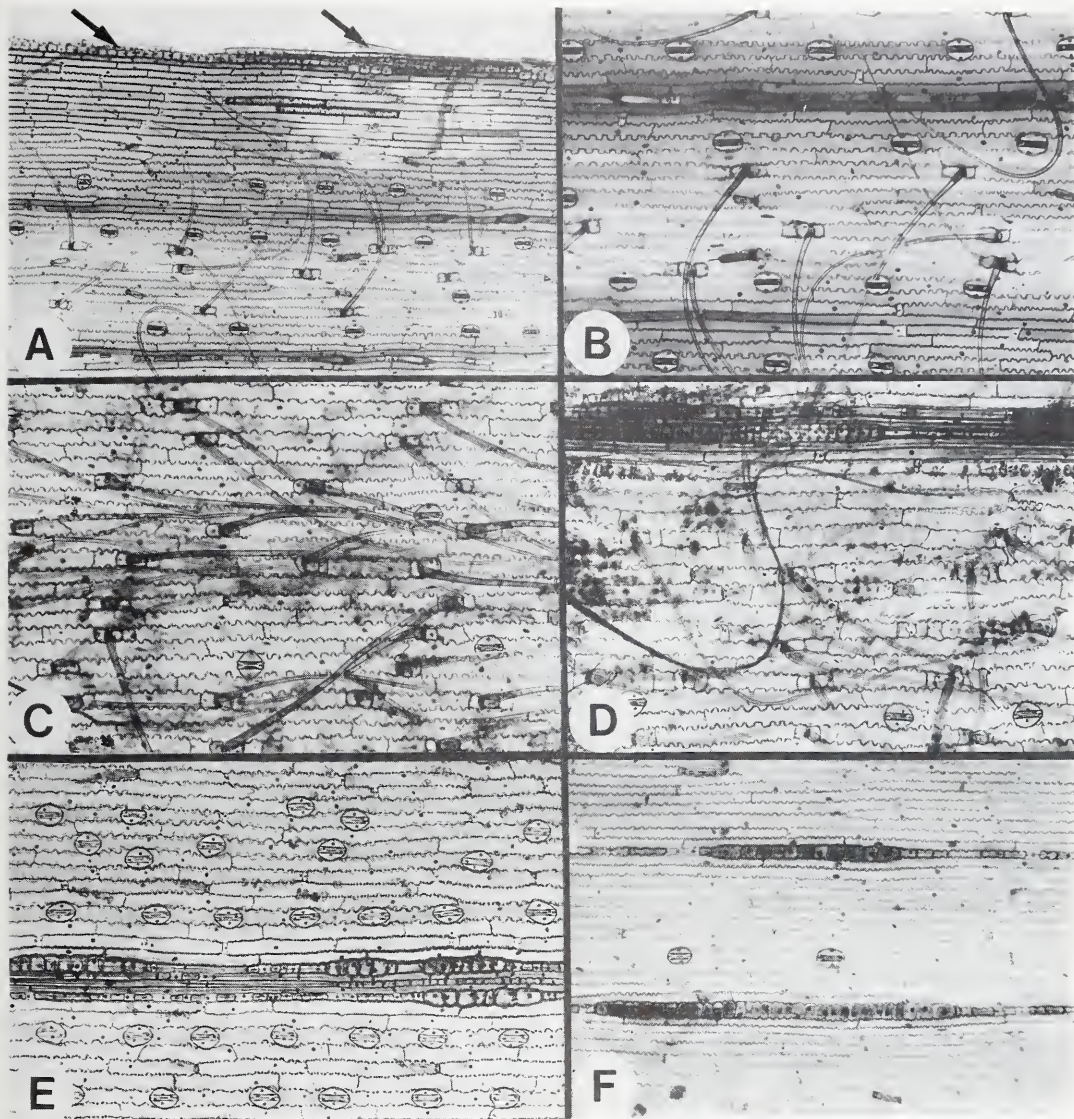


FIGURE 36.2.—*Pentaschistis trisetia*: abaxial epidermal structure. A–E, soft mesic leaves. F, strengthened leaf with supporting tissue.

A, epidermal pattern in region of margin; note linear glands in margin (arrowed) as seen in surface view.

B, detail of soft, flexible macrohairs inserted between two modified epidermal cells, microhairs, dome-shaped stomata and very elongate rectangular long cells with sinuous walls.

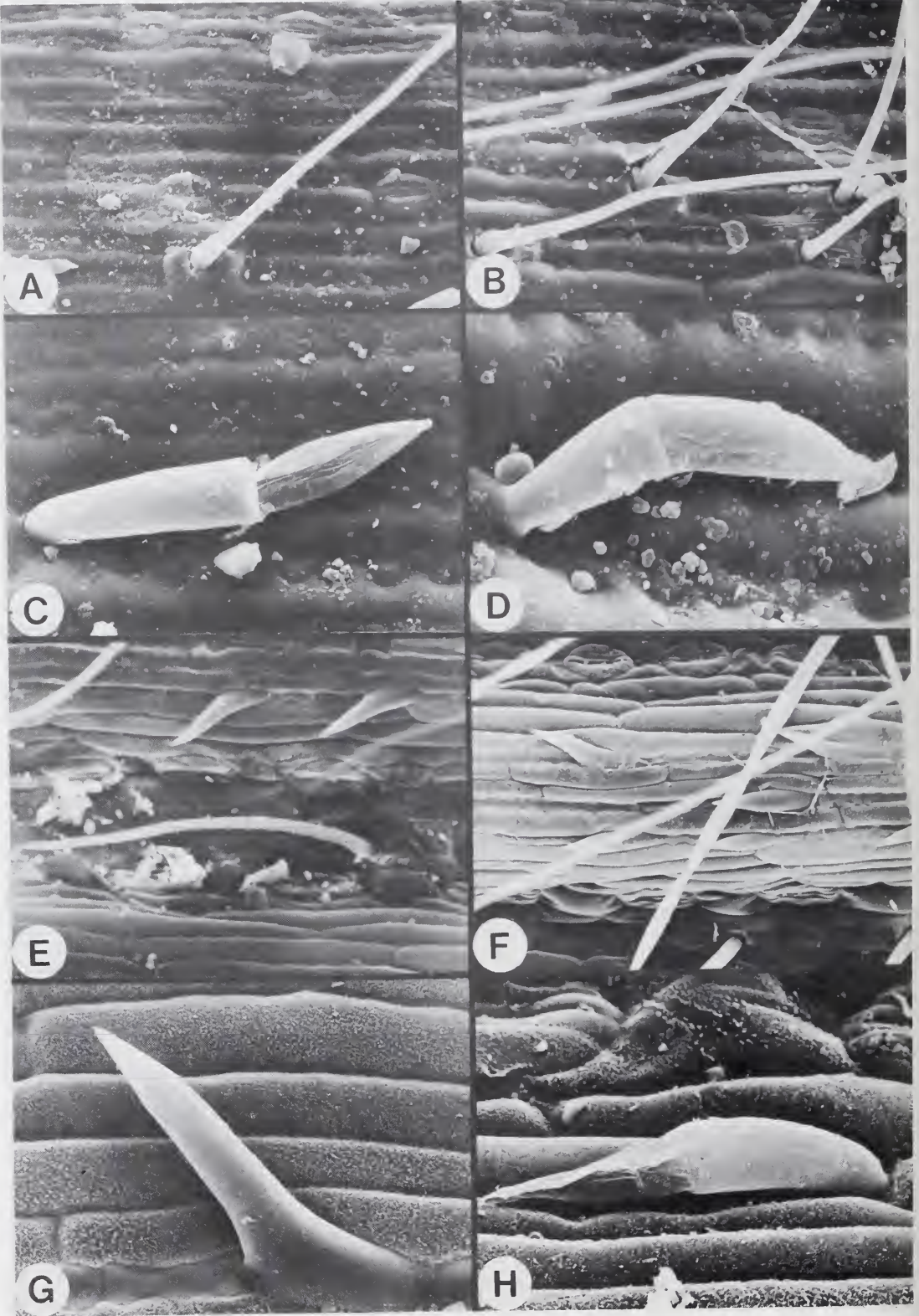
C, specimen with dense covering of macrohairs; note long cell and stomata form and shape.

D, villous leaf blade with uniseriate linear glands in costal zone; gland length variable from 9–32 cells.

E, specimen with short (6–9 cells), uniseriate linear glands in costal zones; note stomata, microhairs, long cells and absence of macrohairs.

F, epidermis of specimen with strengthened leaf; note very few stomata and narrower intercostal long cells; microhairs common and linear glands present even in very narrow costal zones subtending the third order bundles.

A, B, Ellis 5422; C, Ellis 5423; D, Ellis 5426; E, Ellis 5421; F, Ellis 5783. A, $\times 160$; B–F, $\times 250$.



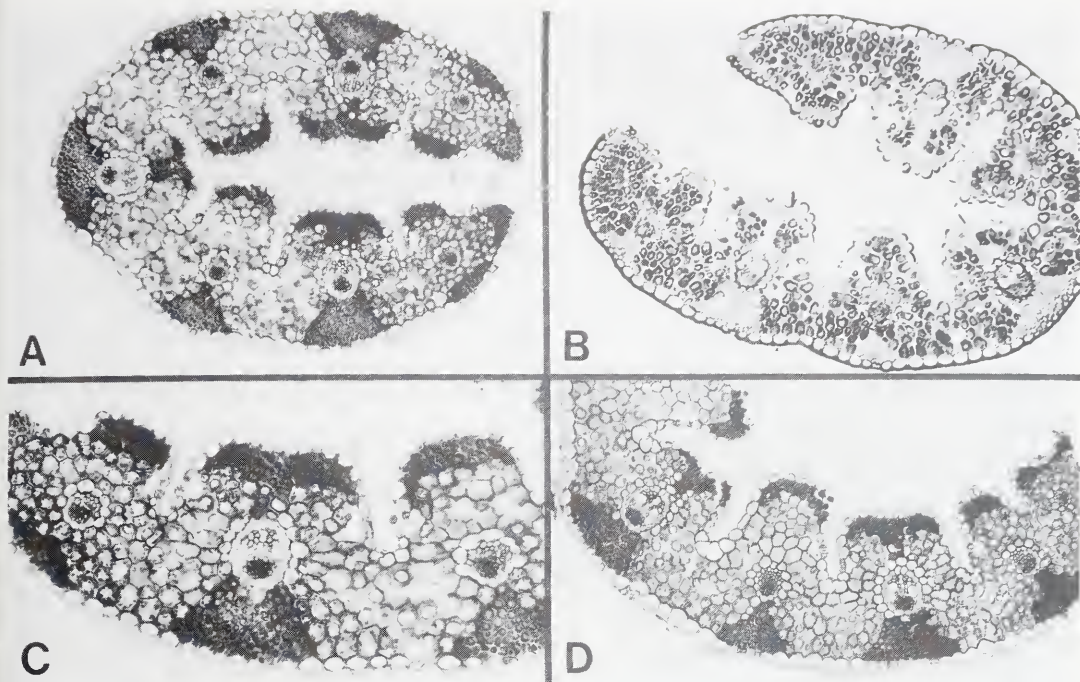


FIGURE 37a.1.—*Pentaschistis rosea* subsp. *rosea*: leaf blade in transverse section.

A, setaceous, permanently infolded outline with only three first order vascular bundles.

B, tightly infolded blade, slightly asymmetrical about the median bundle.

C, detail of rather compact mesophyll with large, angular chlorenchyma cells, sclerenchyma girders and parenchyma sheath cells without chloroplasts.

D, chlorenchyma cells, girders and thick cuticle.

A, C, Ellis 5793; B, Ellis 5797; D, Ellis 5483. A, B, D, $\times 250$; C, $\times 400$.

FIGURE 36.3.—*Pentaschistis trisetata*: epidermal ultrastructure. A–D, abaxial epidermis. E–H, adaxial epidermis.

A, macrohair, stomata and elongated long cells with sinuous walls.

B, macrohairs.

C, microhair with tapering distal cell; two cells comprising hair of similar length.

D, microhair with tapering distal cell; distal cell longer than basal cell.

E, elongated costal prickles and macrohair located in adaxial furrow.

F, adaxial rib with prickles and stomata present on sides of furrow; macrohairs arise from bases of furrows.

G, adaxial prickles with long barb.

H, adaxial microhair with tapering but collapsed distal cell; both cells of similar length.

A, C, E, G, Ellis 5423; B, D, F, H, Ellis 5426. A, B, E, F, $\times 200$; C, G, $\times 650$; D, H, $\times 850$.

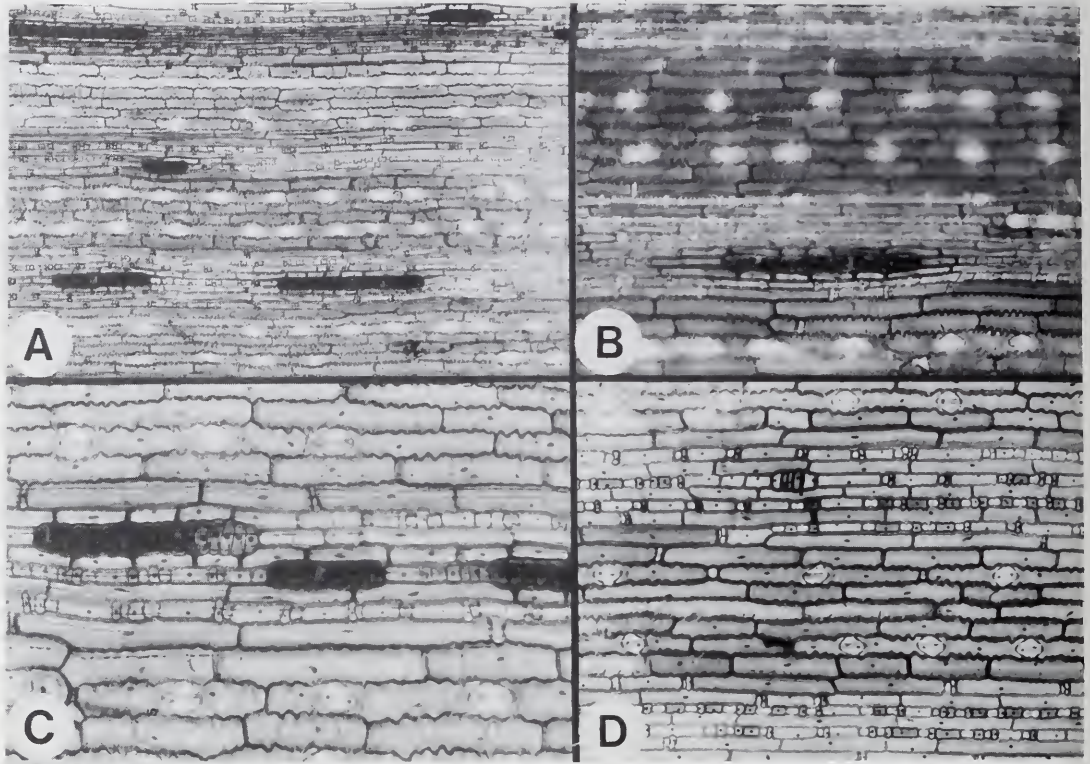


FIGURE 37a.2.—*Pentaschistis rosea* subsp. *rosea*: abaxial epidermis.

A, zonation with intercostal stomata and darkly stained costal linear glands.

B, detail of two costal linear glands and intercostal stomata and microhairs.

C, linear gland detail; note size of gland cells relative to costal long cells and the thick walls of these cells; nuclei are present in the gland cells.

D, specimen with few glands and these very short, of 4–5 very short cells.

A–C, Ellis 5483; D, Ellis 5793. A, $\times 160$; B, D, $\times 250$; C, $\times 400$.

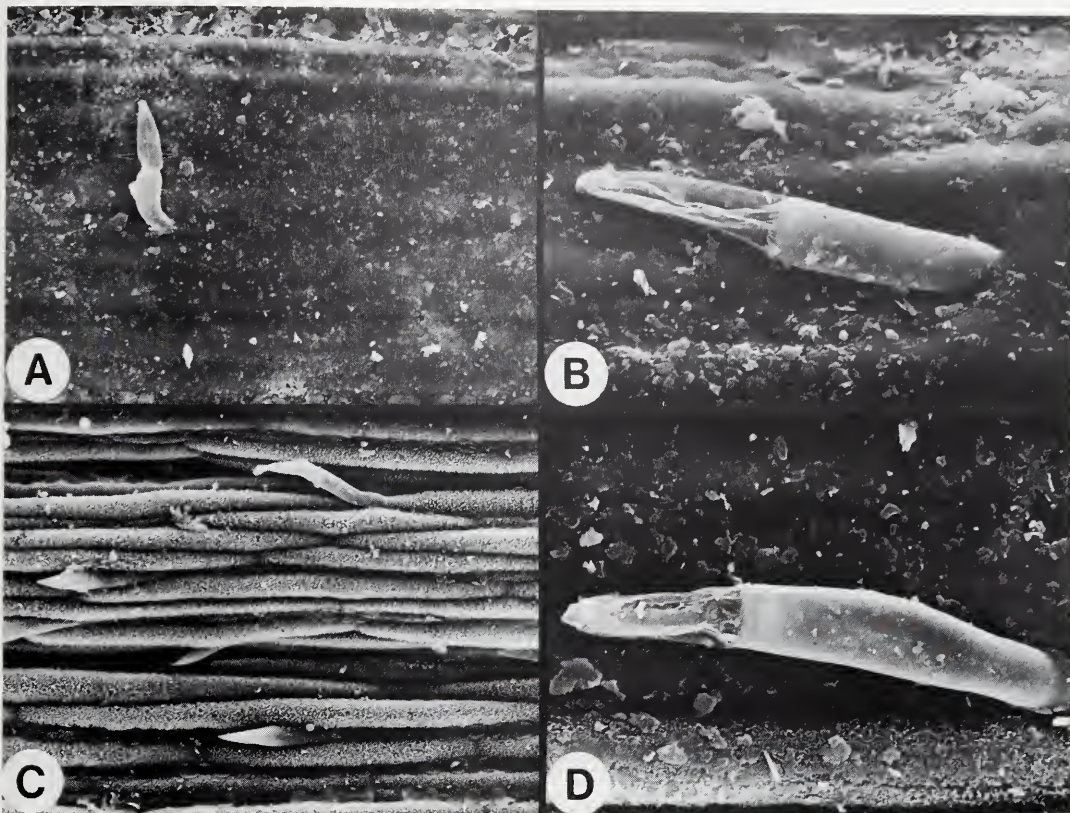


FIGURE 37a.3.—*Pentaschistis rosea* subsp. *rosea*: SEM of leaf epidermides. A, B, abaxial epidermis. C, D, adaxial epidermis.

A, featureless abaxial epidermis with single microhair.

B, microhair detail with tapering distal cell equal in length to basal cell.

C, adaxial costal zone with inflated long cells and shortly barbed prickles.

D, adaxial microhair with distal cell much shorter than basal cell.

A–D, *Ellis* 5483. A, C, $\times 200$; B, $\times 650$; D, $\times 850$.

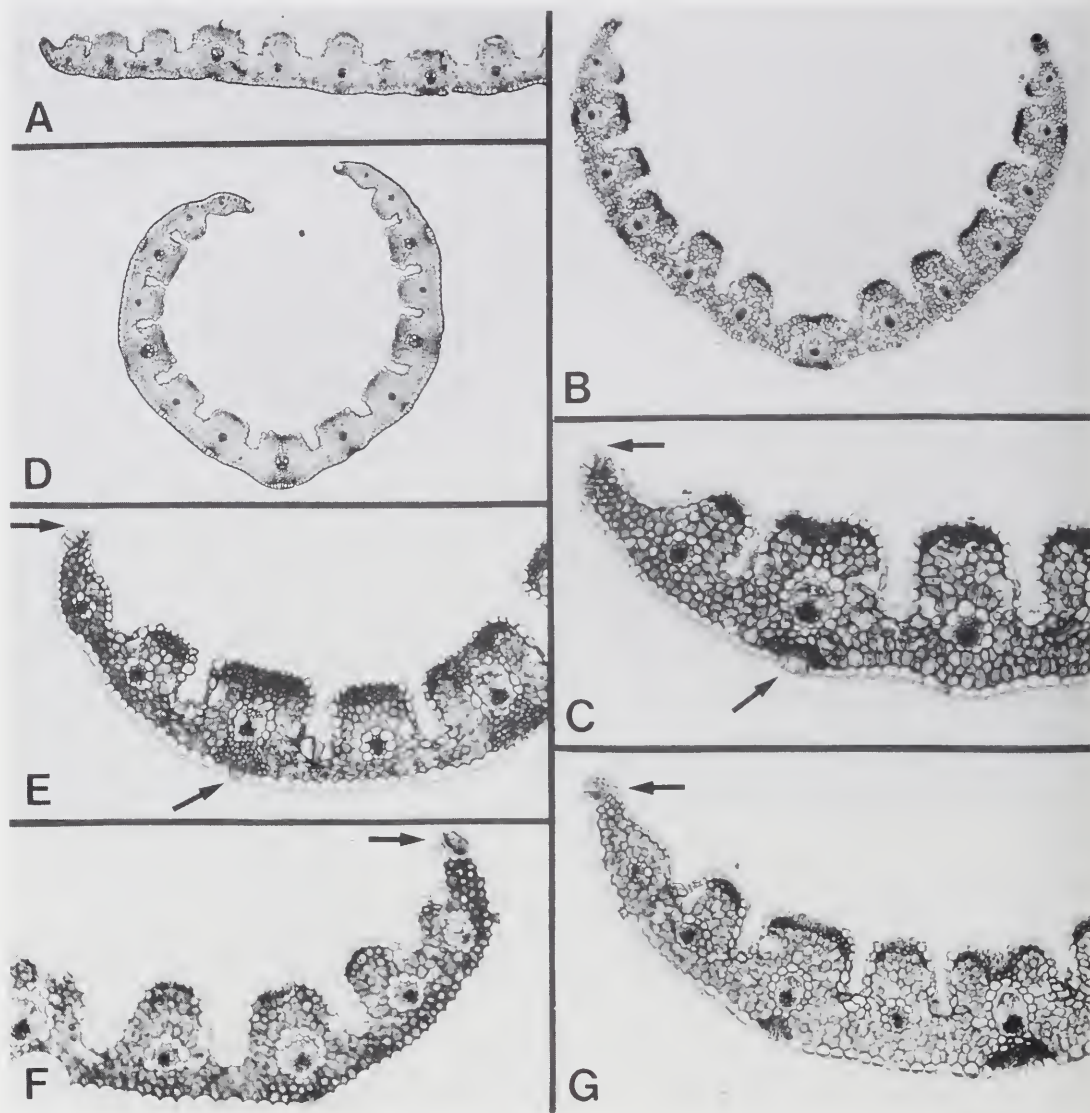


FIGURE 37b.1.—*Pentaschistis rosea* subsp. *purpurascens*: consistent transectional leaf anatomy.

A, flat, expanded leaf outline.

B, broadly infolded blade.

C, detail of projecting margin with linear gland cells (arrowed); linear gland also present opposite first order vascular bundle (arrowed).

D, more tightly infolded blade.

E, narrow, projection as margin with linear gland (arrowed); uniseriate linear glands also present on abaxial costal zones opposite larger bundles (arrowed); note deep adaxial cleft-like furrows and prominent flat-topped ribs.

F, tapering margin with linear gland (arrowed); note compact nature of mesophyll.

G, margin with linear gland (arrowed).

A, *Ellis* 5535; B, C, *Ellis* 5532; D, E, *Ellis* 5580; F, *Ellis* 5800; G, *Ellis* 5514. A, B, D, $\times 100$; C, E–G, $\times 250$.

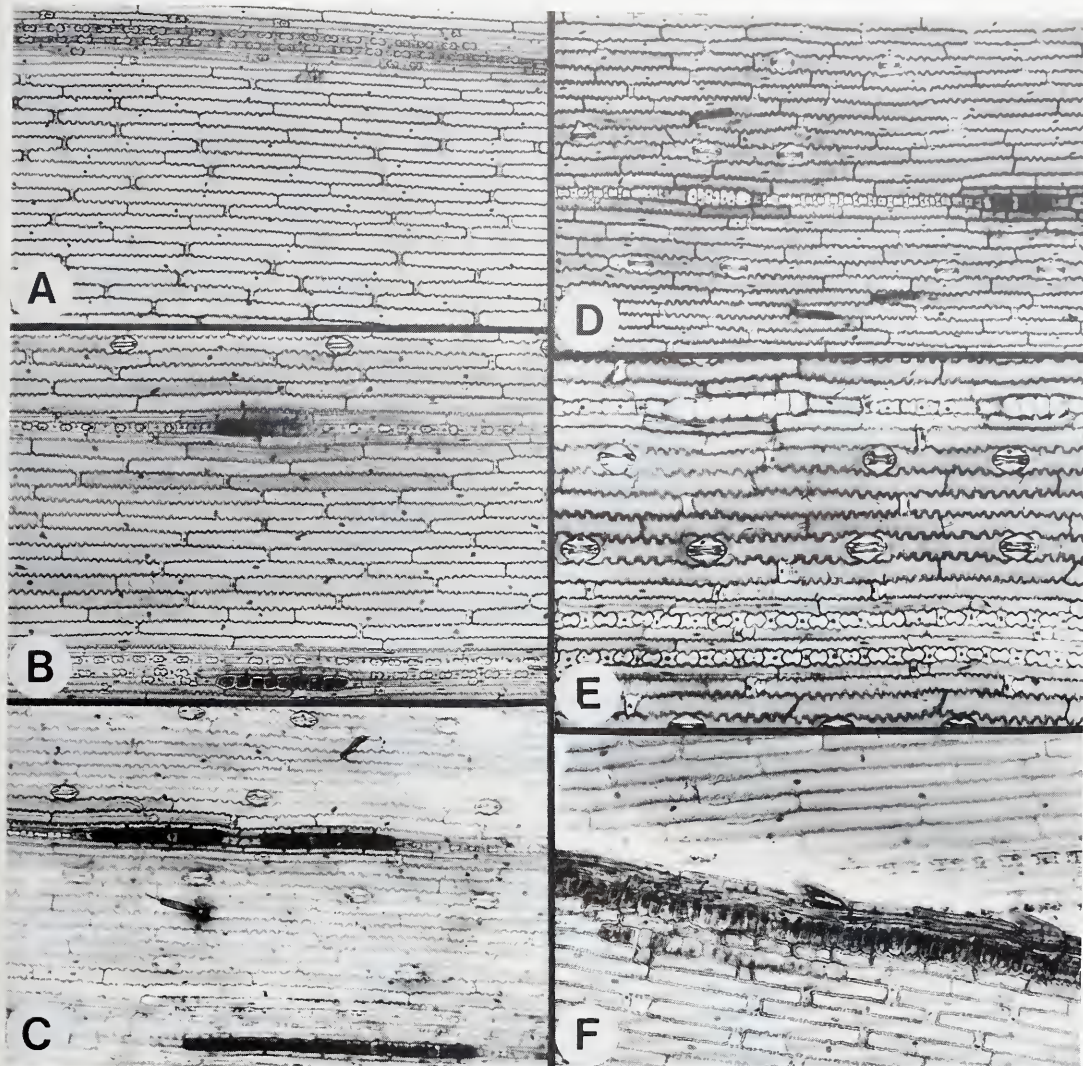


FIGURE 37b.2.—*Pentaschistis rosea* subsp. *purpurascens*: abaxial epidermal structure.

A, epidermal zonation with costal and intercostal zone; note absence of stomata and epidermal appendages.

B, detail of costal zones with irregular dumbbell-shaped silica bodies and uniseriate linear glands; no microhairs and very few stomata.

C, elongate linear glands, microhairs and stomata present.

D, linear glands, microhairs and stomata; long cells slightly sinuous.

E, detail of uniseriate linear glands, silica bodies and sinuous long cell walls.

F, leaf margin showing linear gland and prickly hairs.

A, *Ellis* 5789; B, *Ellis* 5582; C, *Ellis* 5535; D, *Ellis* 5532; E, *Ellis* 5586; F, *Ellis* 5790. A, $\times 160$; B–D, $\times 250$; E, F, $\times 400$.

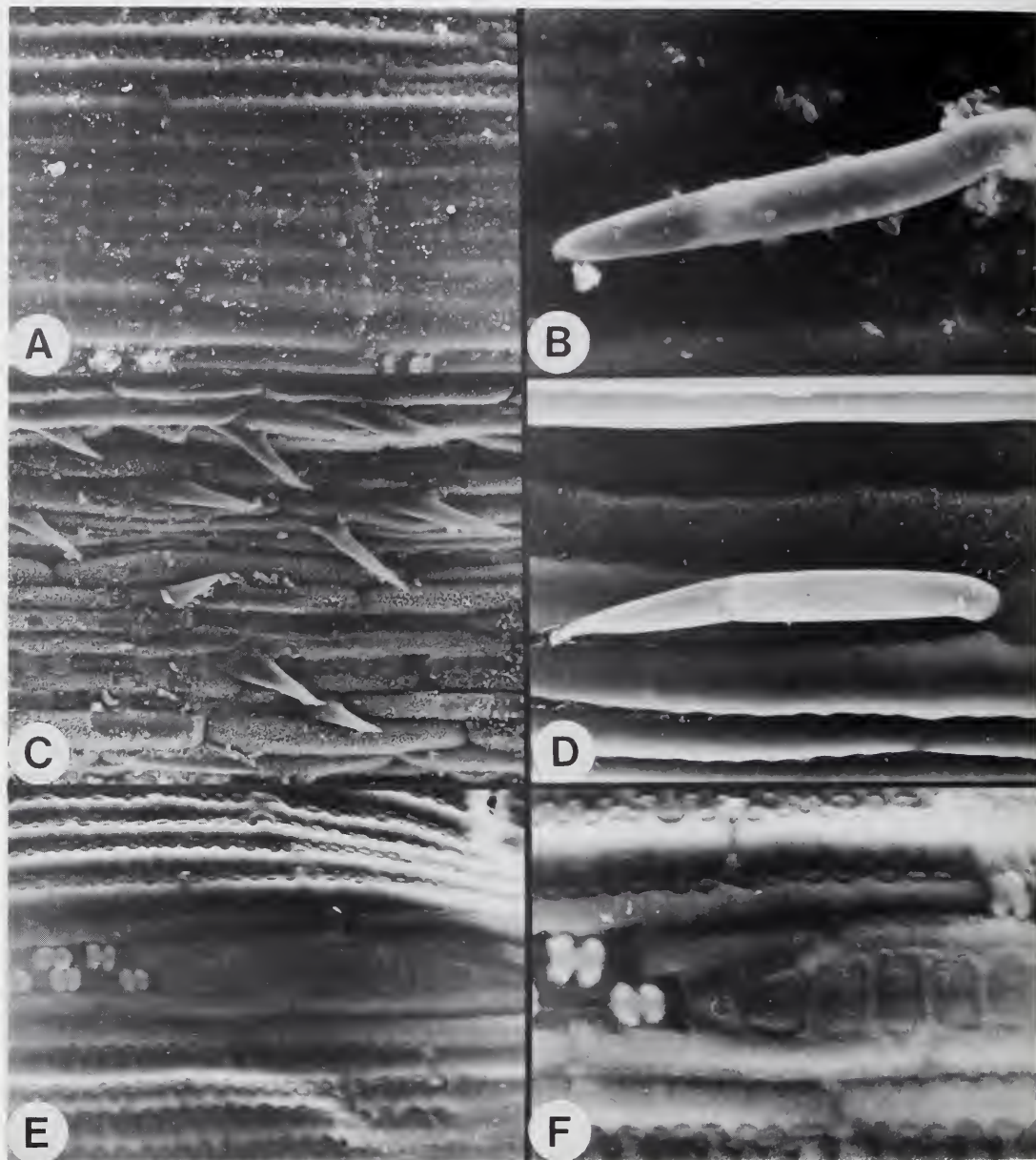


FIGURE 37b.3.—*Pentaschistis rosea* subsp. *purpurascens*: epidermal ultrastructure. A, B, E, F, abaxial epidermis.

C, D, adaxial epidermis.

A, thick, sinuous, long cell walls.

B, microhair with short, tapering distal cell.

C, adaxial rib with prickly hairs.

D, adaxial microhair with pointed distal cell only slightly shorter than basal cell.

E, outline of linear gland cells in costal zone.

F, faint outlines of linear gland cells; note silica bodies and sinuous intercostal long cell walls.

A, D, E, F, *Ellis* 5582; B, *Ellis* 5532; C, *Ellis* 5586. E, $\times 20$; F, $\times 40$; A, C, $\times 200$; B, D, $\times 650$.

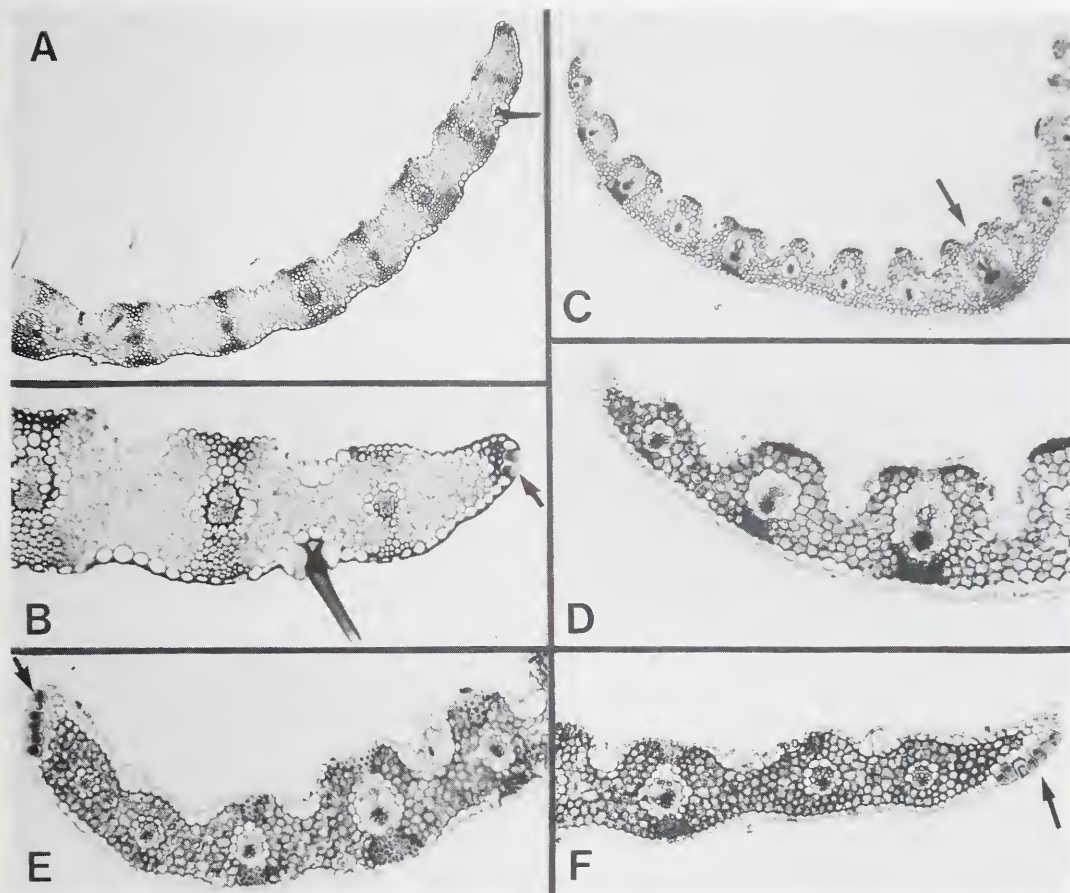


FIGURE 38.1.—*Pentaschistis pseudopallescens*: transectional leaf blade anatomy.

A, broad, expanded leaf blade.

B, detail of lateral part of blade with narrow projecting margin with abaxially situated linear gland cells (arrowed); note macrohair base in section.

C, slightly infolded blade with structurally distinct midrib (arrowed).

D, detail of narrow projection in margin, relatively compact mesophyll, colourless parenchyma sheath cells and thick abaxial cuticle.

E, margin with 6-seriate linear gland (arrowed). F, detail of broad linear marginal gland (arrowed); note adaxial macrohairs.

A, B, *Ellis 5523*; C, D, *Ellis 5565*; E, *Ellis 5796*; F, *Ellis 5501*. A, C, $\times 100$; B, D–F, $\times 250$.

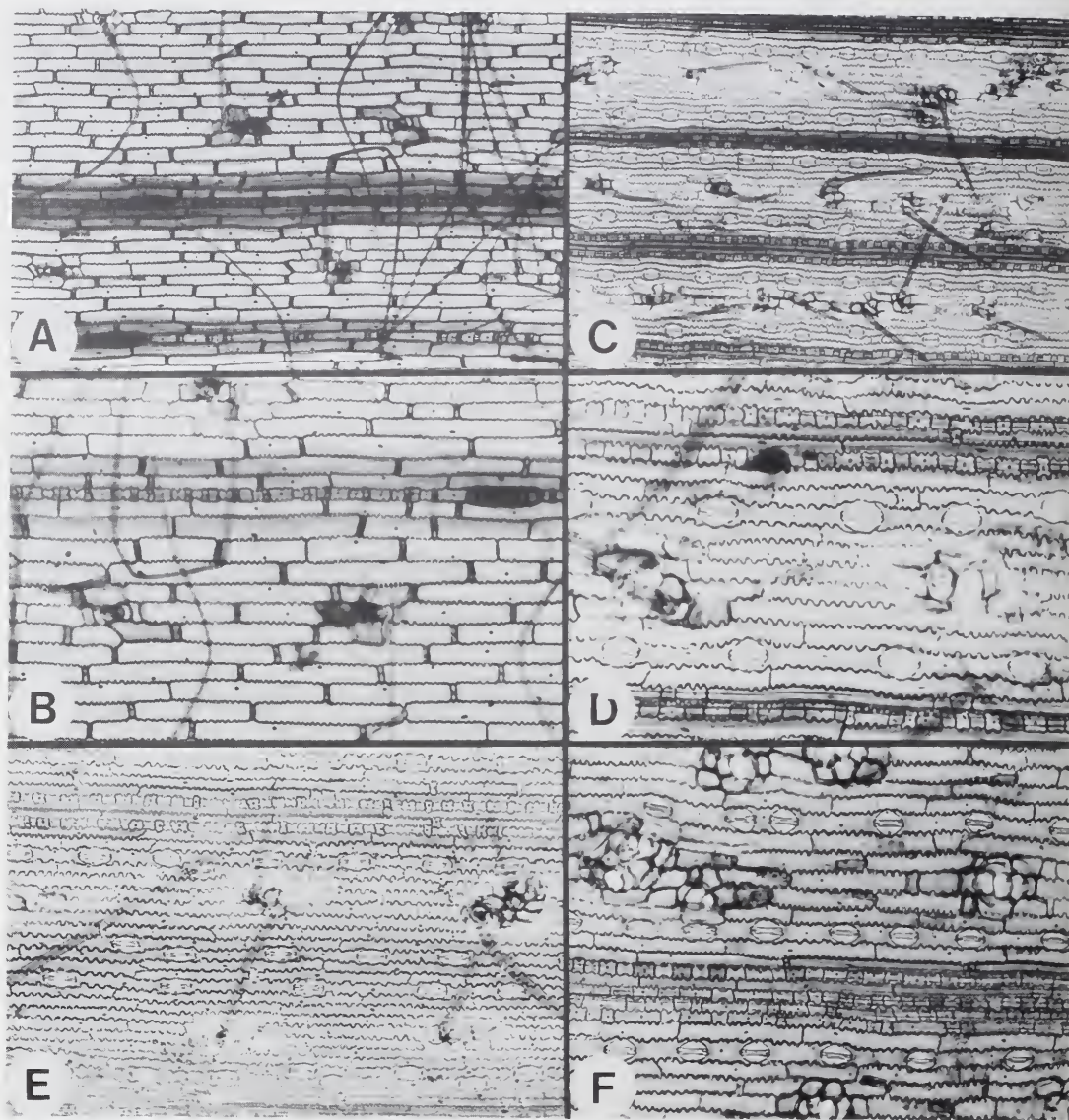


FIGURE 38.2. — *Pentaschistis pseudopallescens*: abaxial epidermal structure. A, B, specimen with anatomy resembling that of *P. pallescens*. C–F, specimens with typical *P. pseudopallescens* anatomy.
 A, epidermal zonation with linear glands on costal zones.
 B, detail of costal linear gland and silica bodies, intercostal long cells and thin, flexible macrohairs; note absence of stomata.
 C, epidermal zonation typical of *P. pseudopallescens*; note absence of linear glands.
 D, detail of silica bodies, stomata, sinuous-walled long cells and short, thick-walled macrohairs embedded in a few raised epidermal cells.
 E, stomata, sinuous long cells and macrohairs.
 F, specimen with stomata, macrohairs and microhairs; note well-differentiated costal zones which do not contain linear glands.
 A, B, Ellis 5565; C, D, Ellis 5501; E, Ellis 5796; F, Ellis 5523. A, C, $\times 160$; B, D–F, $\times 250$.

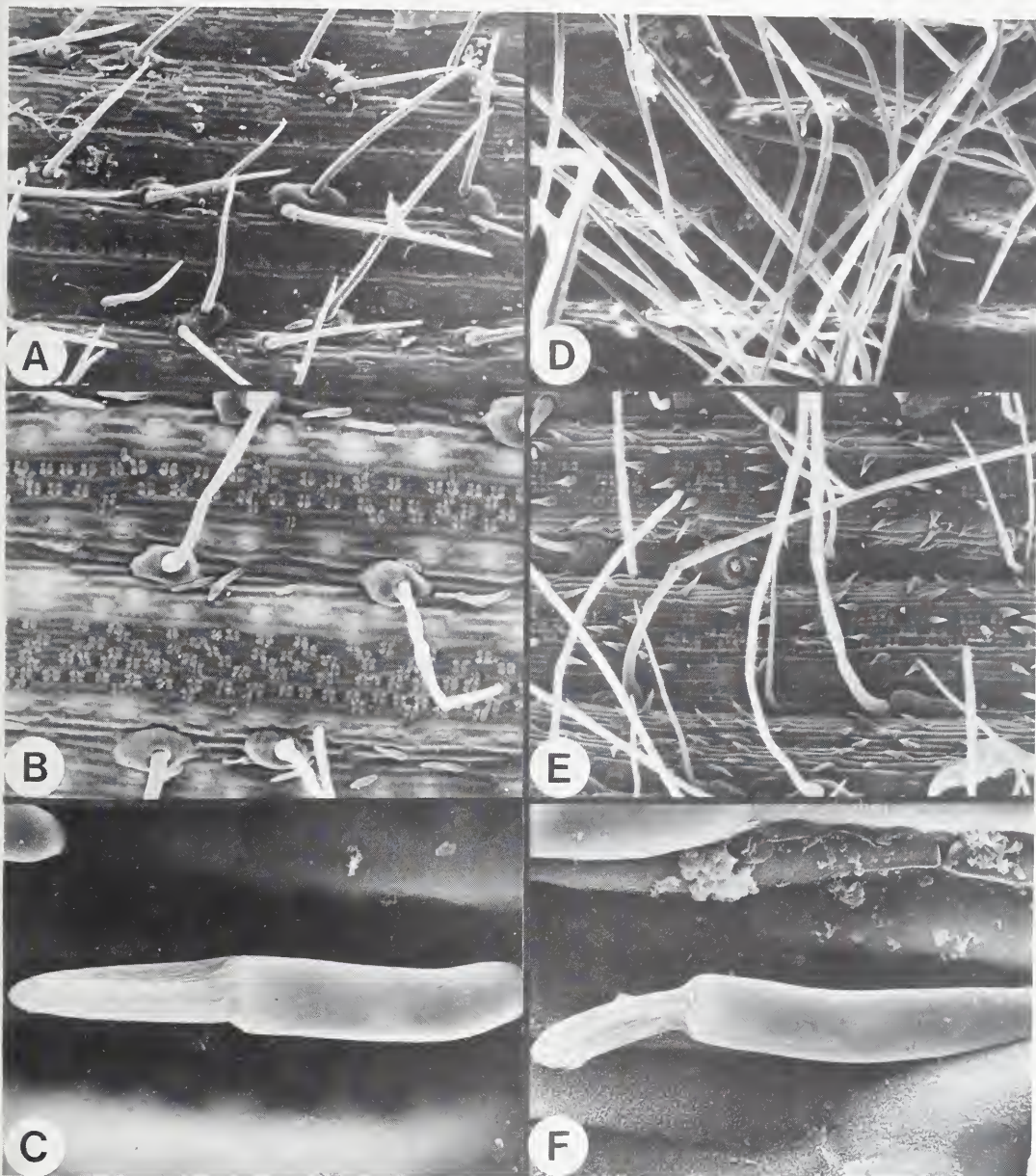


FIGURE 38.3.—*Pentaschistis pseudopallescens*: SEM of epidermides. A–C, abaxial epidermis. D–F, adaxial epidermis.

A, short intercostal macrohairs on raised cushions.

B, cushion-based macrohairs, stomata, microhairs and silica bodies.

C, abaxial microhair with distal cell only slightly shorter than basal cell.

D, denser, longer adaxial macrohairs.

E, adaxial ribs and furrows and macrohairs.

F, adaxial microhair with distal cell much shorter than basal cell.

A, D, *Ellis* 5796; B, C, E, F, *Ellis* 5523. A, B, D, E, $\times 60$; C, $\times 650$; F, $\times 800$.

FIGURE 39.1.—*Pentaschistis pallescens*: transectional leaf anatomy showing characteristic tapering leaf margin which is consistently present in all collections.

A, narrow, projecting margin and well-developed adaxial ribs and furrows.

B, margin a narrow projection.

C, very narrow projection with thickened sclerenchyma tissue as margin; note lateral linear gland (arrowed).

D, narrow projecting margin with uniseriate linear gland (arrowed).

E, narrow projection as margin.

F, typical tapering margin.

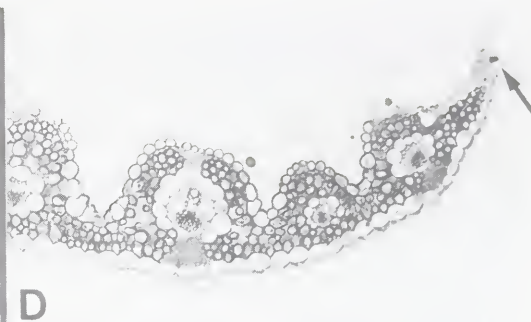
G, anatomical detail of relatively compact mesophyll with angular chlorenchyma cells and conspicuous outer bundle cells devoid of chloroplasts; note large uniform size of abaxial epidermal cells.

H, chlorenchyma, bundle sheath and abaxial epidermal cell detail.

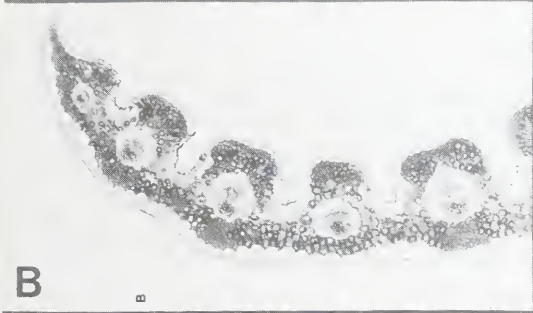
A, *Linder* 4338; B, *Ellis* 2277; C, *Ellis* 2276; D, *Ellis* 2309; E, *Ellis* 2272; F, G, *Ellis* 5537; H, *Ellis* 5573. A, B, $\times 160$; C–H, $\times 250$.



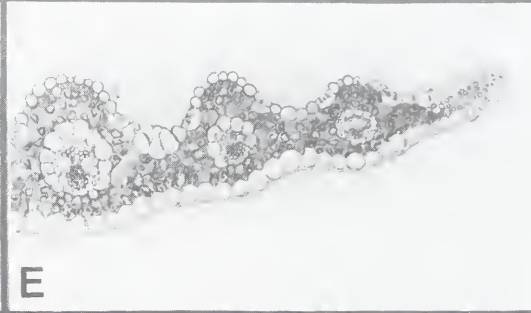
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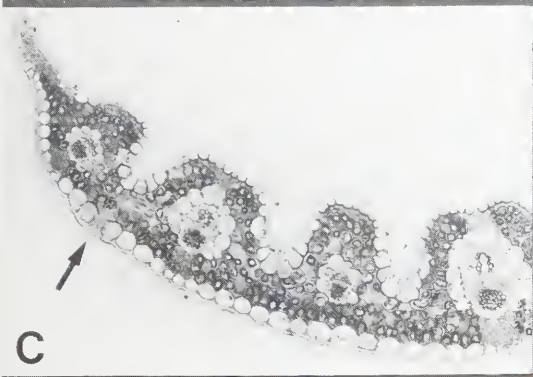
D



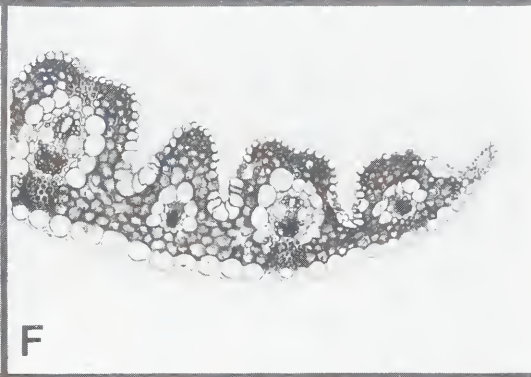
B



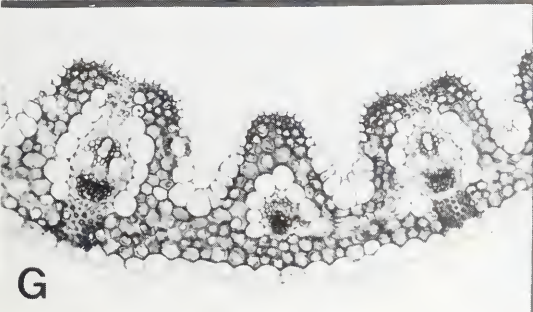
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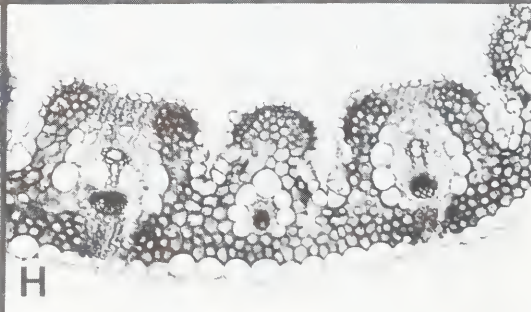
C



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G



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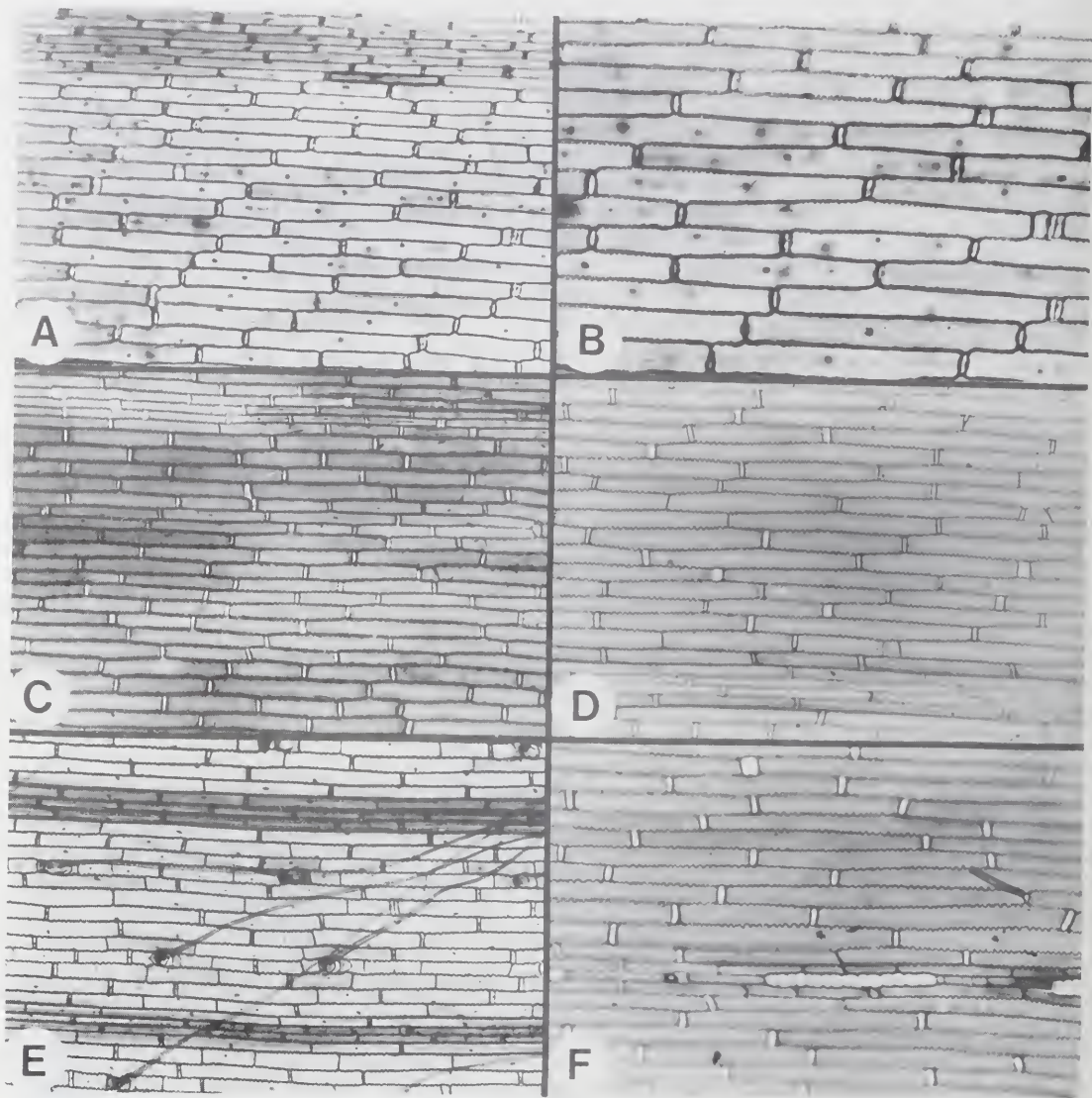


FIGURE 39.2.—*Pentaschistis pallescens*: abaxial epidermal anatomy.

A, epidermal pattern showing very slight distinction between costal and intercostal zone cell structure.

B, intercostal long cell size and form; note straight anticlinal walls and tall and narrow short cells between successive long cells.

C, epidermal zonation virtually indistinguishable.

D, detail of fusiform long cells; note slightly sinuous cell walls.

E, example of specimen with macrohairs with inflated epidermal cell associated with the hair base; costal zones structurally identical to intercostal zones but stain differently.

F, specimen with uniseriate linear gland and microhair.

A, B, Ellis 5572; C, Linder 4338; D, Ellis 2250; E, Ellis 5537; F, Ellis 2309. A, C, E, $\times 160$; B, D, F, $\times 250$.

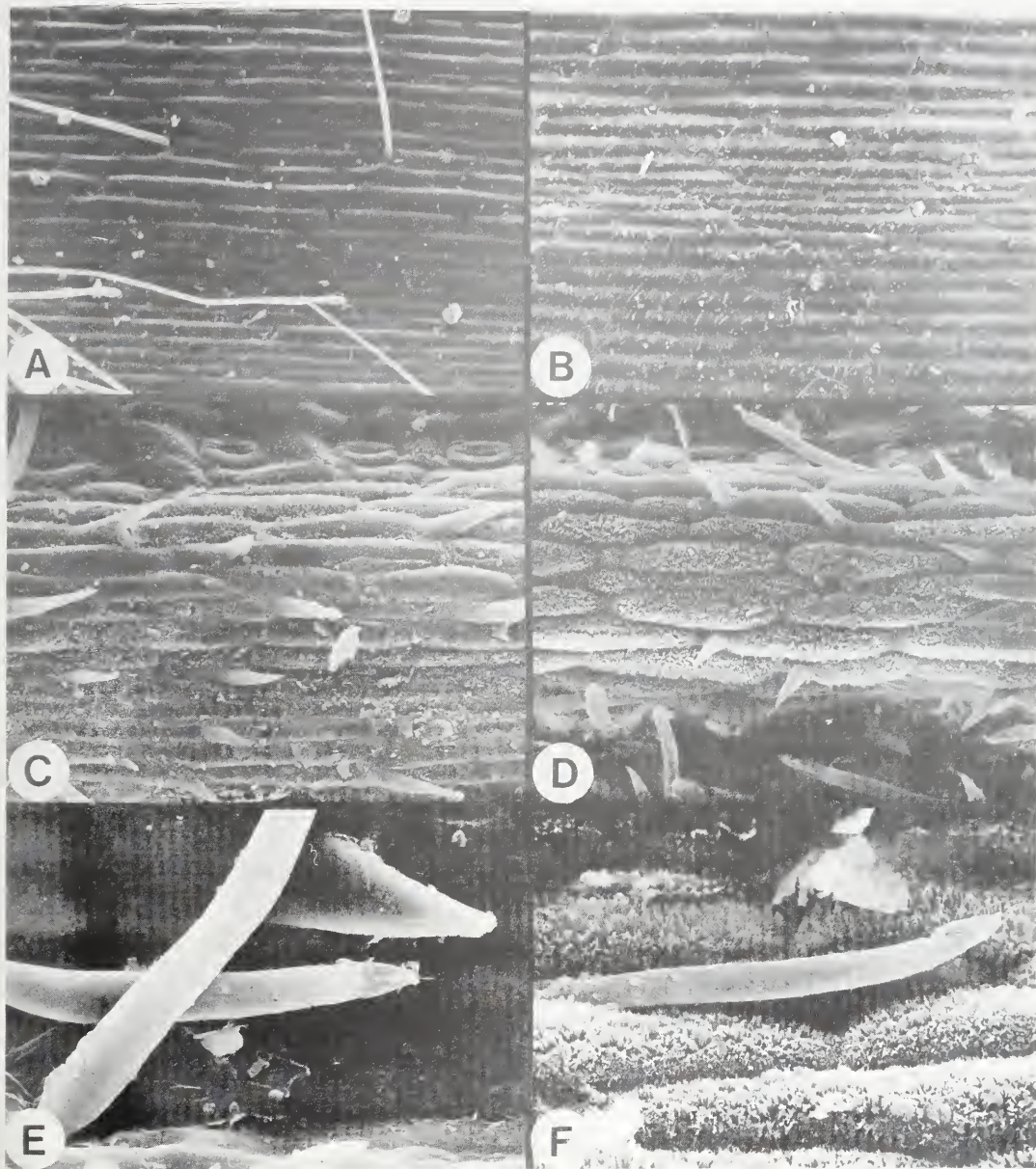


FIGURE 39.3.—*Pentaschistis pallescens*: SEM of abaxial and adaxial leaf blade surfaces. A, B, abaxial epidermis.

C–F, adaxial epidermis.

A, uniform cellular pattern with few macrohairs.

B, featureless abaxial epidermis.

C, adaxial rib with short prickles; note stomata on sides of furrows.

D, inflated fusiform costal long cells; note prickles and microhairs on sides and base of furrow.

E, macrohair base, prickles and microhair in adaxial furrow.

F, detail of thin elongated adaxial microhair with minute distal cell.

A, C, E, *Ellis* 5537; B, D, F, *Ellis* 5572. A, B, $\times 60$; C, D, $\times 200$; E, F, $\times 550$.

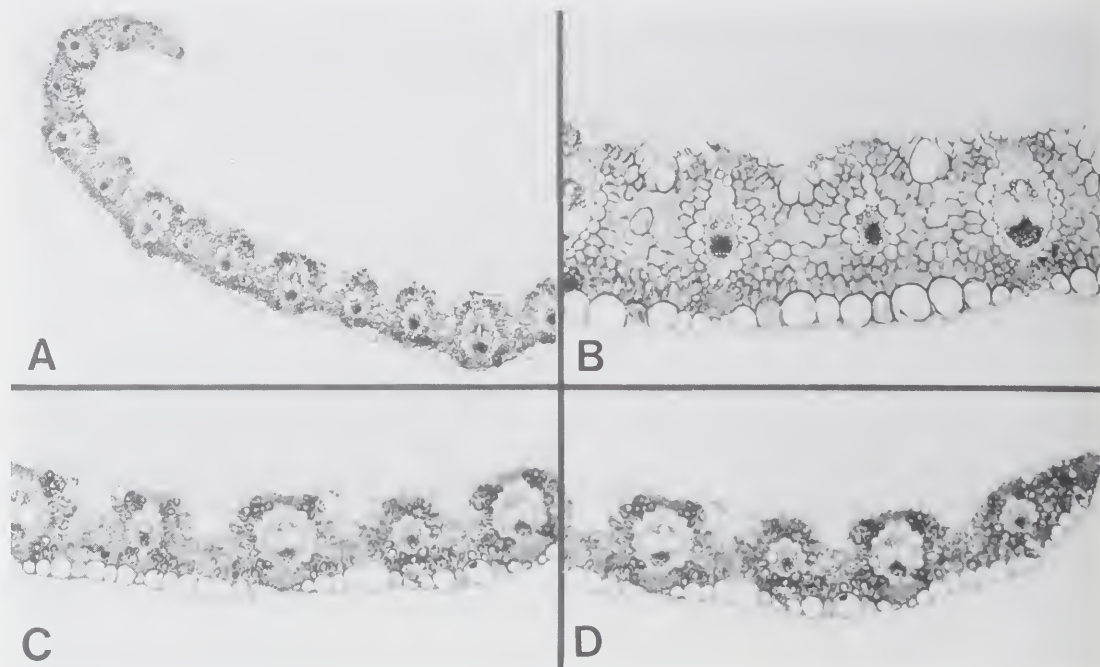


FIGURE 40a.1.—*Pentaschistis aurea* subsp. *aurea*: transectional leaf blade anatomy.

A, slightly inrolled and infolded but expanded blade; midrib not differentiated and margin is distinctly tapering.
B, detail of rather compact chlorenchyma, colourless outer bundle sheath cells and abaxial epidermal cells considerably larger than adaxial ones.

C, colourless parenchyma sheath cells, dense chlorenchyma and large abaxial epidermal cells.

D, pointed, tapering leaf margin.

A, *Ellis* 5570; B, *Ellis* 5539; C, D, *Ellis* 5822. A, $\times 100$; B–D, $\times 250$.

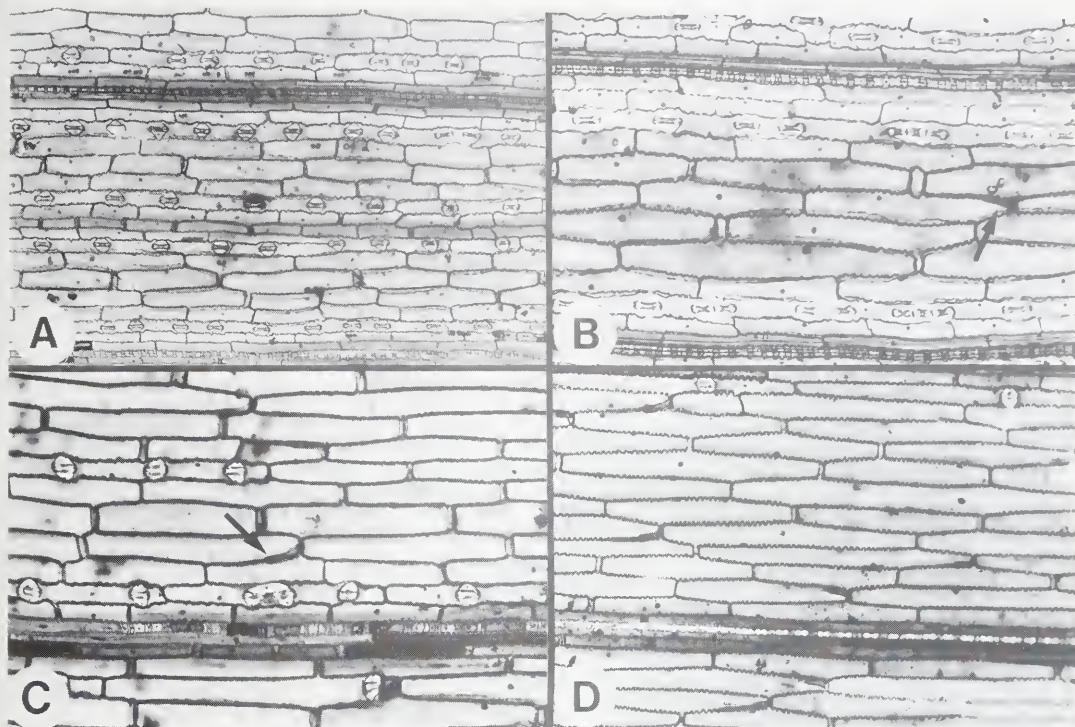


FIGURE 40a.2.—*Pentaschistis aurea* subsp. *aurea*: abaxial epidermal cellular arrangement.

A, epidermal zonation with narrow costal zones.

B, detail of irregularly dumbbell-shaped silica bodies and fusiform intercostal long cells; note large number of longitudinally fused stomata.

C, fusiform long cells, deformed stomata and microhair (arrowed).

D, specimen with very few stomata; long cells fusiform in shape.

A, B, *Ellis* 5570; C, *Ellis* 5539; D, *Ellis* 5822. A, $\times 160$; B–D, $\times 250$.

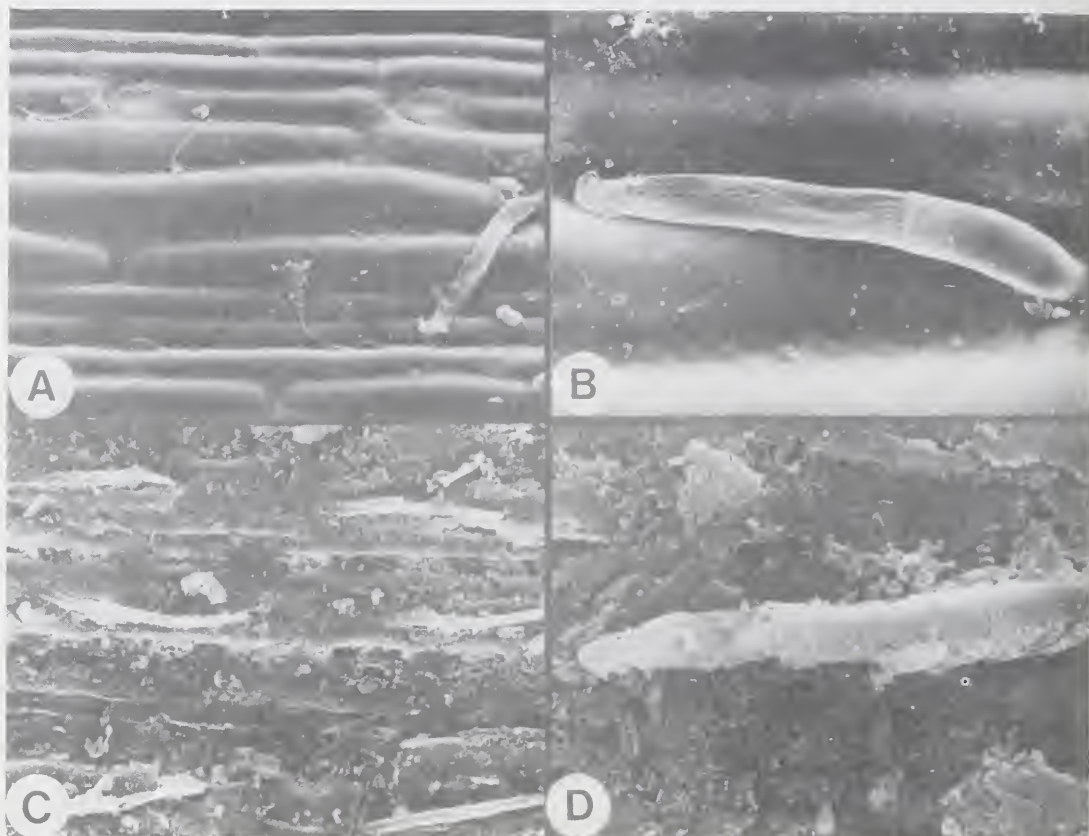


FIGURE 40a.3.—*Pentaschistis aurea* subsp. *aurea*: epidermal ultrastructure. A, B, abaxial epidermis. C, D, adaxial epidermis.

A, fusiform long cells, stomata and microhair.

B, microhair with distal cell twice as long as basal cell.

C, adaxial surface with elongated microhairs and thick wax layer.

D, detail of microhair with distal cell shorter than basal cell.

A–D, *Ellis* 5539. A, C, $\times 200$; B, $\times 550$; D, $\times 768$.

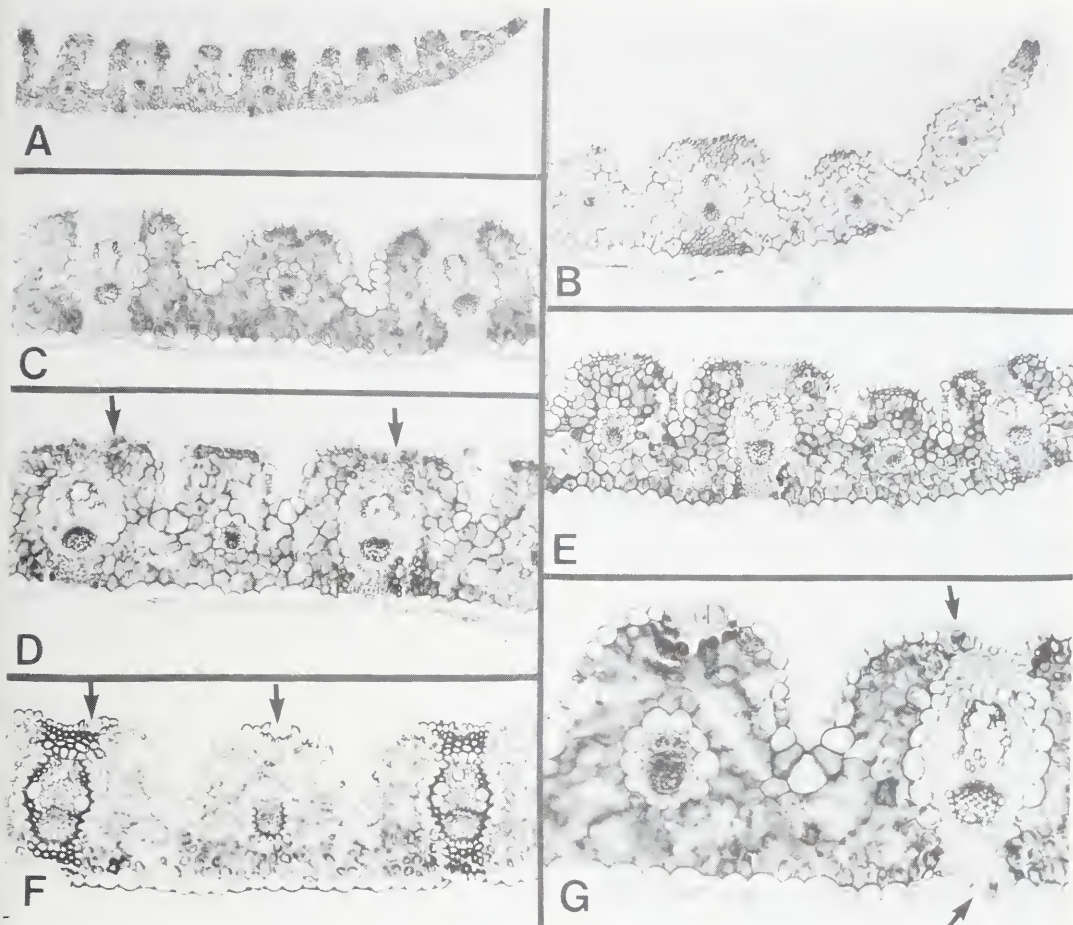


FIGURE 40b.1.—*Pentaschistis aurea* subsp. *pilosogluma*: transverse sections of the leaf blade.

A, lateral part of leaf blade showing tapering margin.

B, detail of narrow, projecting margin.

C, adaxial ribs and furrows, compact mesophyll and well-developed sclerenchyma girders.

D, more diffuse mesophyll; note gland cells on adaxial surface on ribs (arrowed).

E, angular mesophyll cells and colourless outer bundle sheath cells.

F, diffuse mesophyll and adaxial gland cells (arrowed).

G, detail of mesophyll, outer bundle sheath cells and adaxial and abaxial glands (arrowed).

A, *Ellis 5616*; B, *Ellis 5699*; C, *Ellis 3162*; D, *Ellis 5716*; E, *Ellis 5708*; F, *Ellis 5716*; G, *Ellis 5730*. A, $\times 100$;

B–F, $\times 250$; G, $\times 400$.

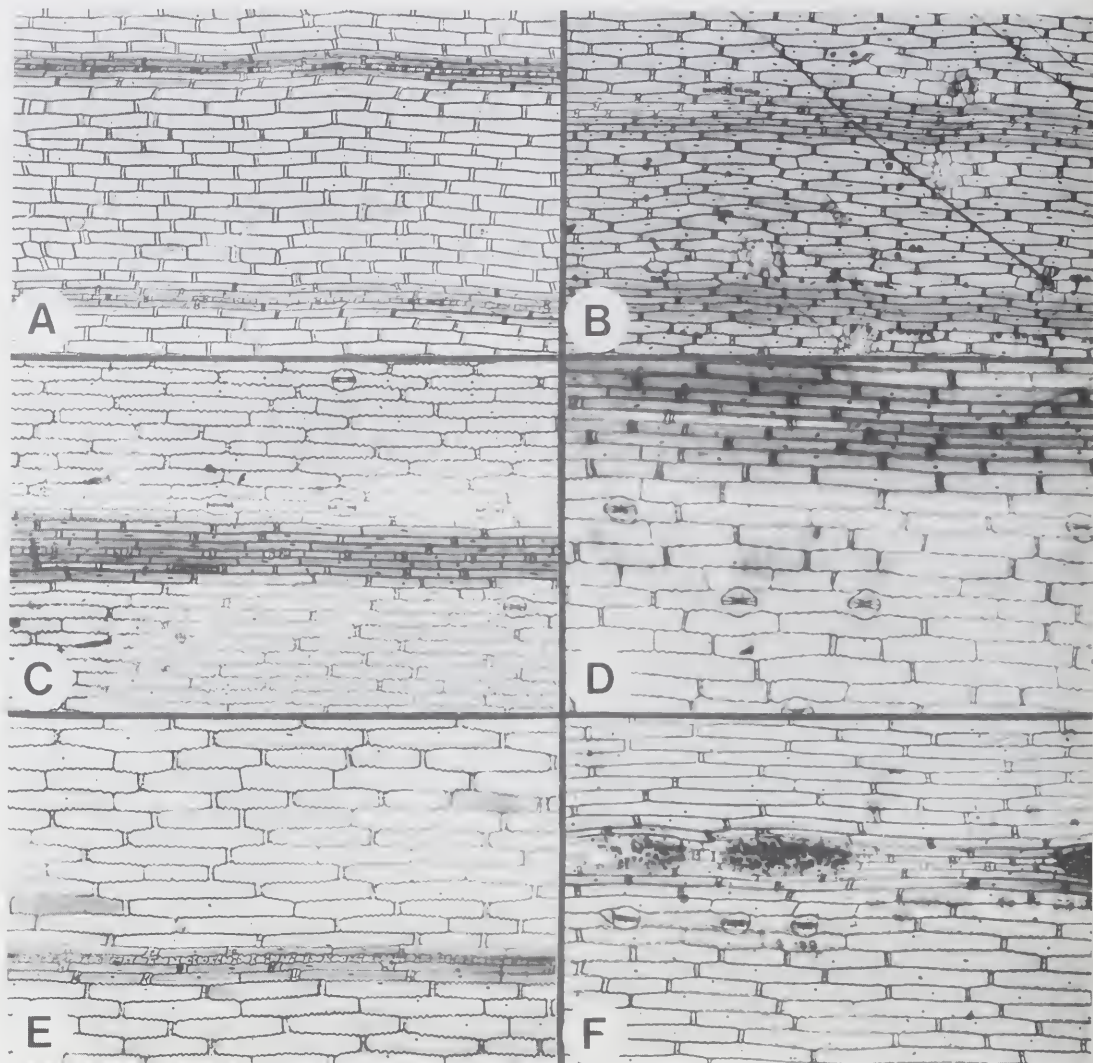


FIGURE 40b.2.—*Pentaschistis aurea* subsp. *pilosogluma*: abaxial epidermis.

A, epidermal pattern with costal and intercostal zones distinguishable; note absence of stomata.

B, epidermal pattern with thin macrohairs on lateral parts of leaf; stomata absent.

C, intermediate specimen from eastern Cape with few stomata and microhairs.

D, another eastern Cape specimen also with stomata.

E, detail of typical epidermis with fusiform, slightly sinuous long cells separated by tall and narrow short cells with no stomata and microhairs; silica bodies variable dumbbell-shaped.

F, elliptical costal glands not raised above leaf surface; few stomata present.

A, *Ellis* 5708; B, *Ellis* 5699; C, *Ellis* 5617; D, *Ellis* 5616; E, *Ellis* 5716; F, *Ellis* 5730. A, B, $\times 160$; C–F, $\times 250$.

FIGURE 40b.3.—*Pentaschistis aurea* subsp. *pilosogluma*: SEM of leaf blade surfaces. A, B, abaxial epidermis. C–H, adaxial epidermis.

A, fusiform intercostal long cells.

B, fusiform long cells with no stomata or microhairs.

C, adaxial ribs with short prickly hairs and microhairs.

D, adaxial rib with sessile elliptical gland present in centre of rib.

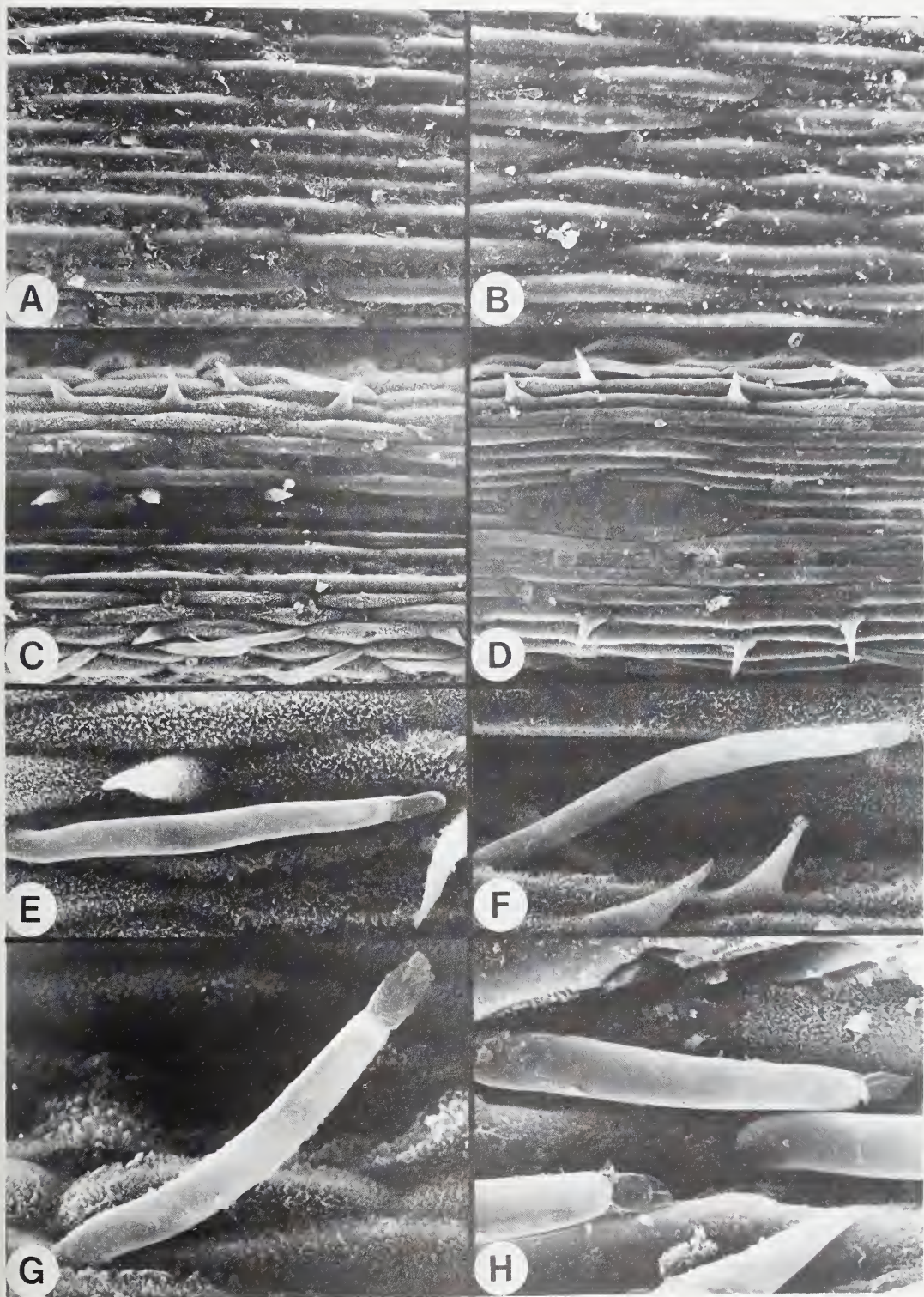
E, slender adaxial microhair with very short distal cell.

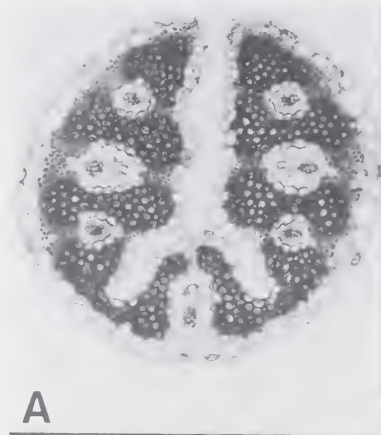
F, another example of slender microhair with minute distal cell.

G, thicker microhair but distal cell still very small.

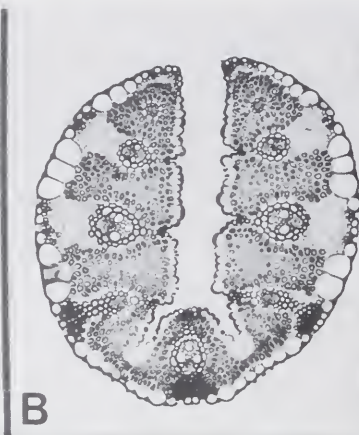
H, microhairs with short distal cells at base of adaxial furrow.

A, H, *Ellis* 5616; B, *Ellis* 5730; C, G, *Ellis* 5716; D, *Ellis* 5617; E, *Ellis* 5699; A–D, $\times 200$; E, F, $\times 550$; G, $\times 800$; H, $\times 850$.





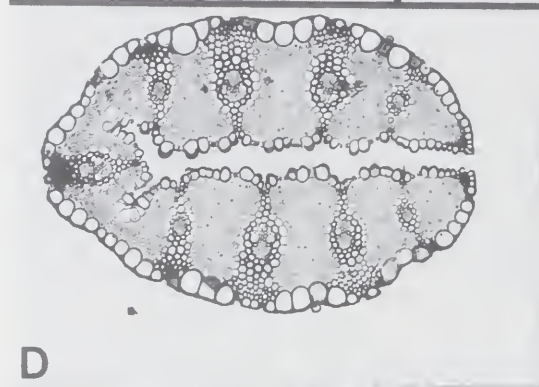
A



B



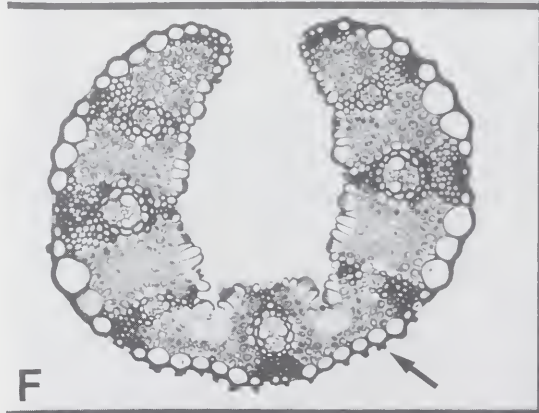
C



D



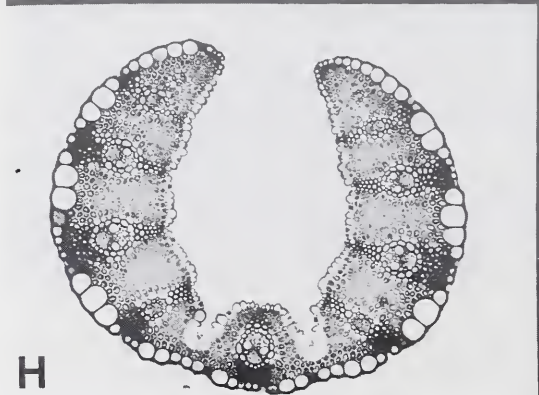
E



F



G



H



I

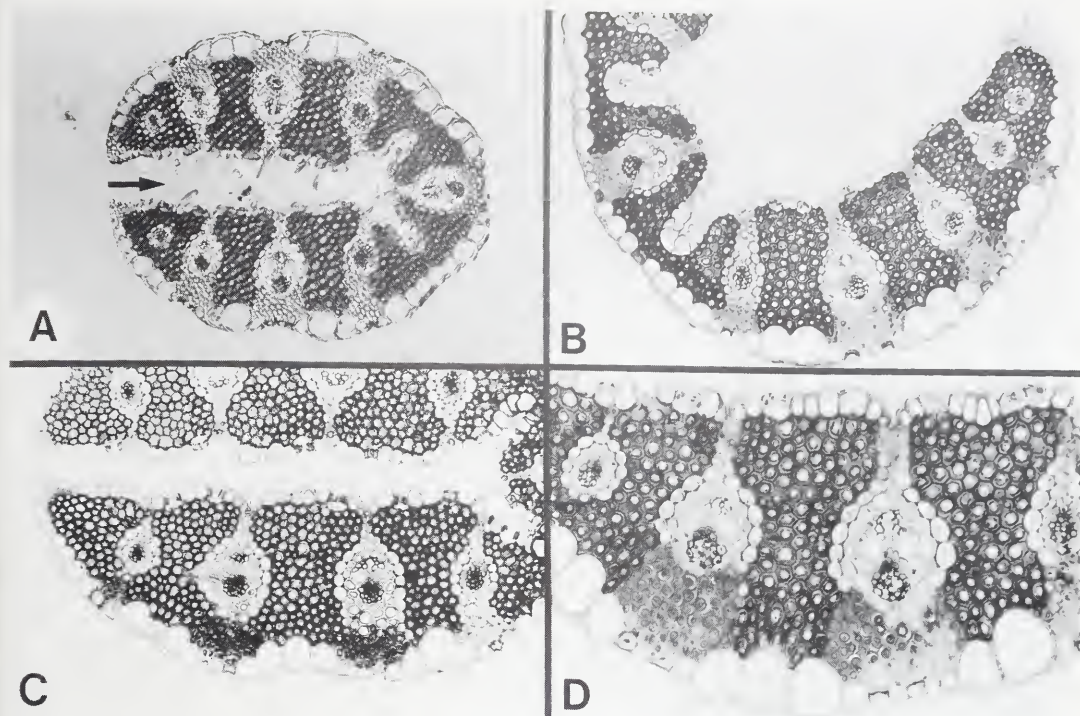


FIGURE 41.2.—*Pentaschistis colorata*: detail of transectional leaf anatomy.

A, a very narrow, filiform leaf with elliptical outline and narrow adaxial furrow; note prickly hairs in this furrow (arrowed); mesophyll compact and parenchyma sheath cells colourless and conspicuous although they are smaller than the mestome sheath cells.

B, canaliculate leaf type showing very compact mesophyll tissue, sclerenchyma girders and the size difference between the adaxial and the abaxial epidermal cells; note that lateral first order bundles are not interspaced by smaller bundles.

C, detail of isodiametric chlorenchyma cells and vascular tissue with narrow metaxylem vessels; note papillate adaxial epidermal cells and difference in leaf blade size to that illustrated in A.

D, cellular detail of mesophyll, sclerenchyma girders, vascular tissue and both epidermides.

A, *Ellis* 2296; B, *Ellis* 2545; C, *Ellis* 5551; D, *Ellis* 2541. A–C, $\times 250$; D, $\times 400$.

FIGURE 41.1.—*Pentaschistis colorata*: variation in the leaf outline from circular to elliptical setaceous type to canaliculate inrolled leaf type; note abaxial intercostal epidermal cells consistently larger than the adaxial epidermal cells. A–C, permanently inrolled leaf with circular outline and deep, narrow adaxial channel; 3 first order bundles and 4 small third order bundles. D, E, acicular leaves with elliptical outlines but adaxial groove still cleft-like; 3 first order bundles but the smaller bundles of similar size which lack protoxylem; an additional pair of bundles may be present. F–I, canaliculate leaf outlines with wide adaxial channels. F, G, leaves with abaxial papillae (arrowed) and 7 bundles. H, I, leaves without abaxial papillae and with 9 bundles in leaf blade.

A, abaxial epidermal cells with thick cuticle, papillate adaxial epidermal cells.

B, fibres of sclerenchyma girders either lignified (e.g. the median bundle) or not.

C, contrast in size between costal and intercostal abaxial epidermal cells very marked.

D, 9 vascular bundles in section.

E, 7 bundles in section.

F, specimen from same locality as circular leaf A above.

G, wide adaxial channel with vertical sides, compound papillae (arrowed).

H, sides of adaxial channel bowed and abaxial epidermal cell size differences very marked.

I, canaliculate outline with rounded channel.

A, *Ellis* 2496; B, *Ellis* 2539; C, *Ellis* 2295; D, *Ellis* 5551; E, *Ellis* 5536; F, *Ellis* 2498; G, *Ellis* 2350; H, *Ellis* 2545;

I, *Ellis* 2217. B, D, E, H, I, $\times 160$; A, C, F, G, $\times 250$.

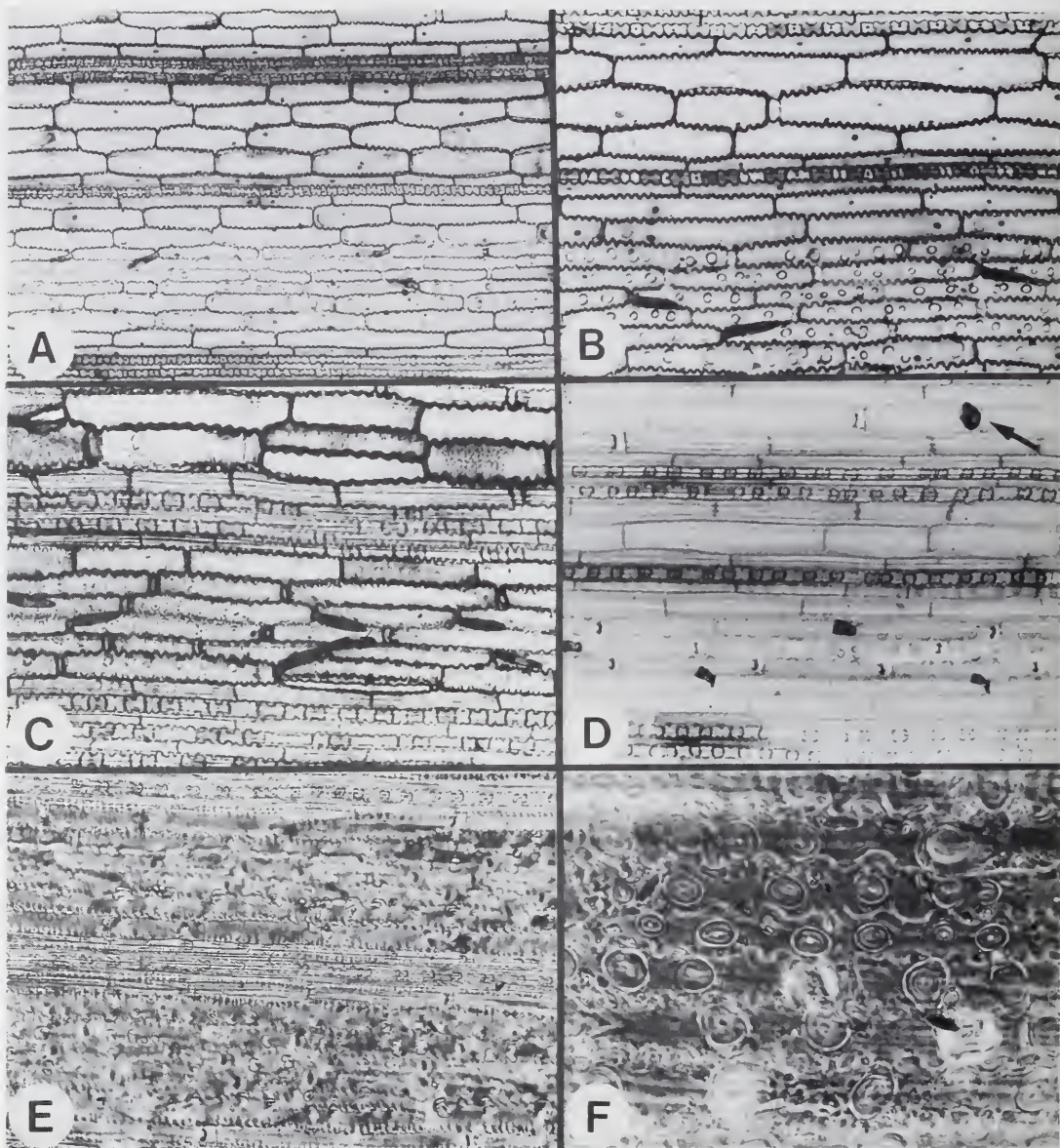


FIGURE 41.3.—*Pentaschistis colorata*: epidermal structure of specimens with papillate abaxial epidermis. A, papillate intercostal zones on either side of costal zone associated with median vascular bundle (lowermost in illustration). B, detail of cuticular papillae in single files on intercostal long cells; note microhairs with rather short distal cells, dumbbell-shaped silica bodies and fusiform long cells with sinuous walls. C, papillate long cells although papillae difficult to distinguish; microhairs with basal cells slightly shorter than distal cells. D, indistinct papillae, dumbbell-shaped silica bodies and inflated basal cells of microhairs (arrowed). E, interference contrast of cuticular papillae showing very thick walls and wart-like appearance of apex. F, detail of cuticular papillae; note very thick walls. A, B, *Ellis* 5445; C, *Ellis* 2539; D, *Ellis* 2496; E, *Ellis* 2350; F, *Ellis* 2217. A, $\times 160$; B–E, $\times 250$; F, $\times 1000$.

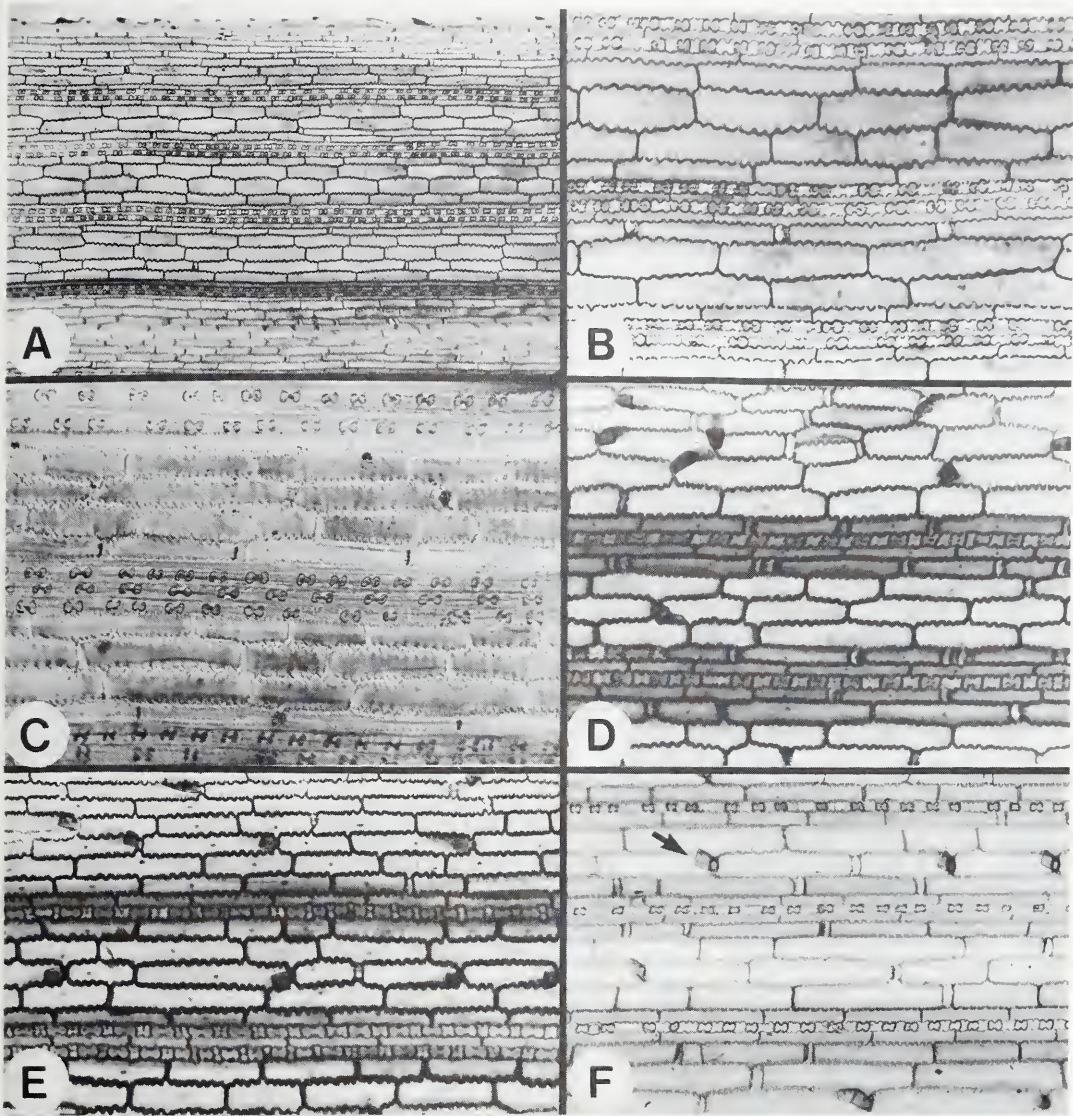


FIGURE 41.4.—*Pentaschistis colorata*: abaxial epidermis of specimens without papillae.

A, epidermal zonation with intercostal long cells much wider than costal cells; note intercostal zones on either side of median bundle (lowermost on illustration) with much narrower long cells than those more laterally located; small prickles in margin.

B, detail of sinuous long cells and dumbbell-shaped silica bodies.

C, interference contrast of dumbbell silica bodies and wide long cells with sinuous walls.

D, costal and intercostal zones with numerous short microhairs with distal cells longer than basal cells.

E, numerous microhairs with tapering distal cells longer than inflated basal cells.

F, silica bodies and basal cells of microhairs; note rare three-celled hair (arrowed).

A, B, *Ellis* 2259; C, *Ellis* 2541; D, *Ellis* 5551; E, *Ellis* 5563; F, *Ellis* 2269. A, $\times 100$; B–F, $\times 250$.

FIGURE 41.5.—*Pentascistis colorata*: SEM of specimens with papillate abaxial epidermis. A, B, E, F, abaxial epidermis. C, D, G, H, adaxial epidermis.

A, compound papillae on intercostal long cells; note microhairs in central intercostal files.

B, detail of cuticular papillae and microhair with distal cell longer than basal cell.

C, adaxial surface with stomata sunken between inflated long cells; note short costal hooks and small macrohair.

D, detail of stoma, inflated long cells and microhair with elongated, tapering distal cell.

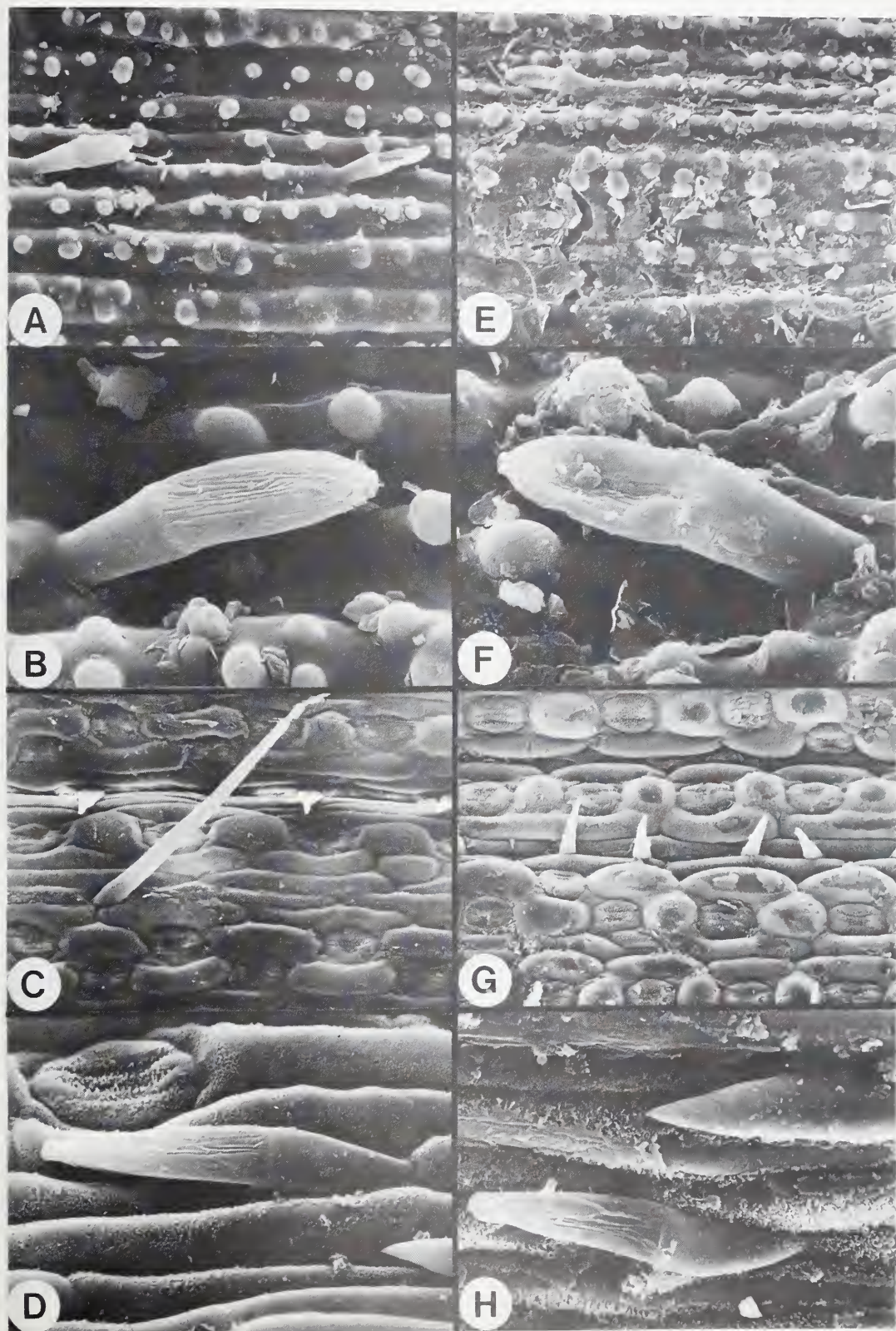
E, abaxial surface with papillae and thick cuticle.

F, microhair with basal and distal cells of equal length.

G, inflated papillae on adaxial surface; note prickles and stomata sunken between inflated papillae.

H, narrower adaxial microhair with distal cell elongated and tapering.

A–D, *Ellis* 5536; E–H, *Ellis* 5445. A, C, E, G, $\times 200$; B, D, H, $\times 700$; F, $\times 800$.



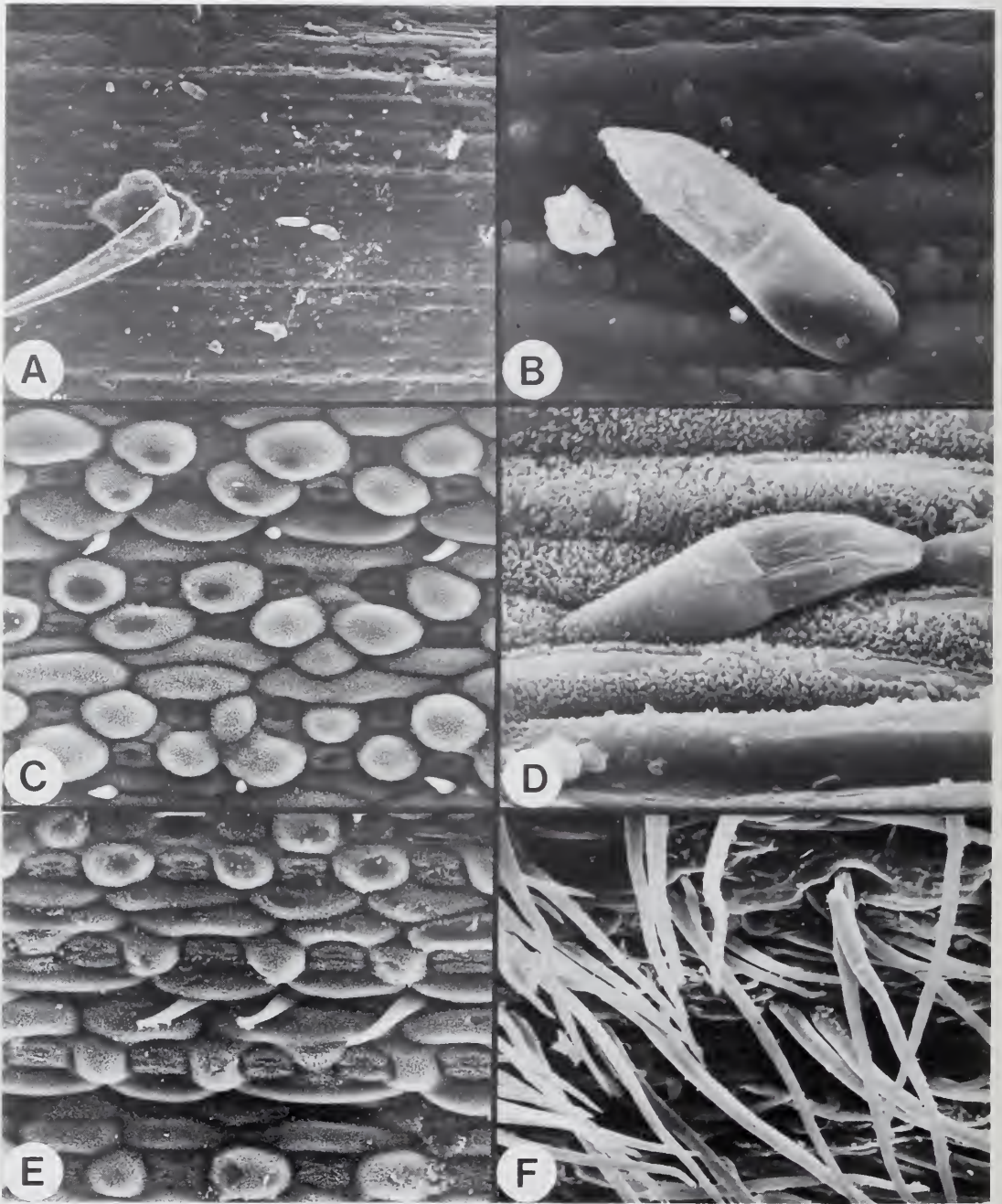


FIGURE 41.6.—*Pentaschistis colorata*: epidermal ultrastructure of specimens without abaxial papillae. A, B, abaxial epidermis. C–F, adaxial epidermis.

A, featureless surface with cushion-based macrohair and small, inflated microhairs.

B, detail of microhair.

C, papillate adaxial epidermis with inflated papillae over arching stomata.

D, adaxial microhair.

E, intercostal long cells and interstomatal cells inflated papillate and over arching the stomata; note small hooks.

F, specimen with unusual adaxial surface covered in macrohairs; inflated papillae do not appear to be present.

A–C, *Ellis 5551*; D, E, *Ellis 5546*; F, *Ellis 5438*. A, $\times 60$; C, E, F, $\times 200$; B, $\times 700$; D, $\times 900$.

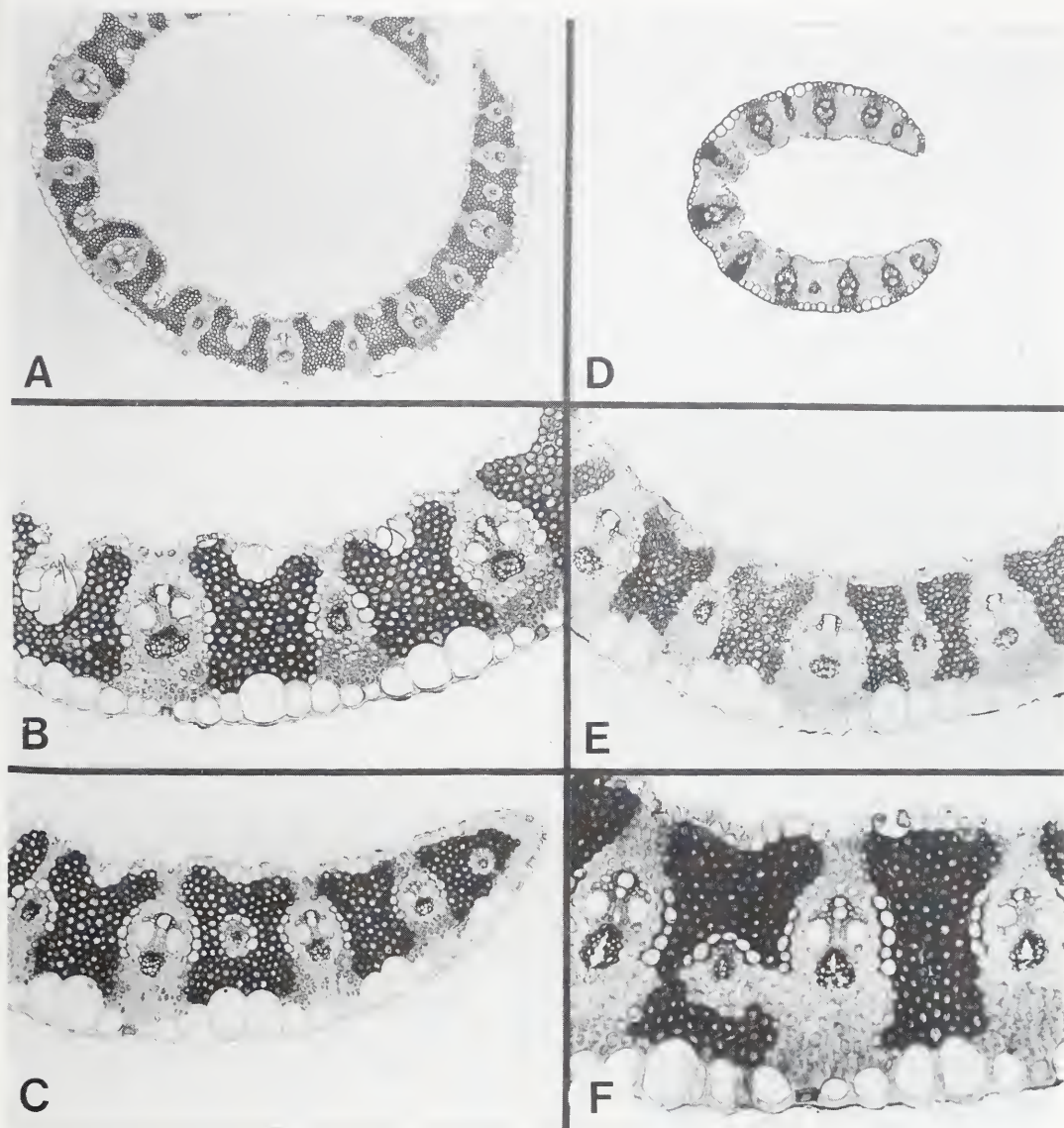


FIGURE 42.1.—*Pentaschistis tortuosa*: anatomy of the leaf blade as seen in transverse section.

A, wide, inrolled outline with adaxial furrows on either side of median bundle well developed; alternating sequence of first order and smaller bundles across blade.

B, detail of lateral part of blade where adaxial furrow development is not present; note single third order bundle between successive first order bundles.

C, anatomy of leaf margin; note very large abaxial intercostal cells.

D, narrow, more setaceous blade resembling the canaliculate condition in *P. colorata*.

E, alternating bundles and clear size difference between adaxial and abaxial epidermal cells.

F, cellular detail of large, thick-walled abaxial epidermal cells and smaller, inflated adaxial epidermal cells; note wide interruptions of outer bundle sheath due to sclerenchyma girder insertion and compact mesophyll of small, isodiametric cells with centrally positioned vacuoles.

A, B, *Ellis* 2227; C, F, *Ellis* 2226; D, *Ellis* 5607; E, *Ellis* 2260. A, D, $\times 100$; B, C, E, $\times 250$; F, $\times 400$.

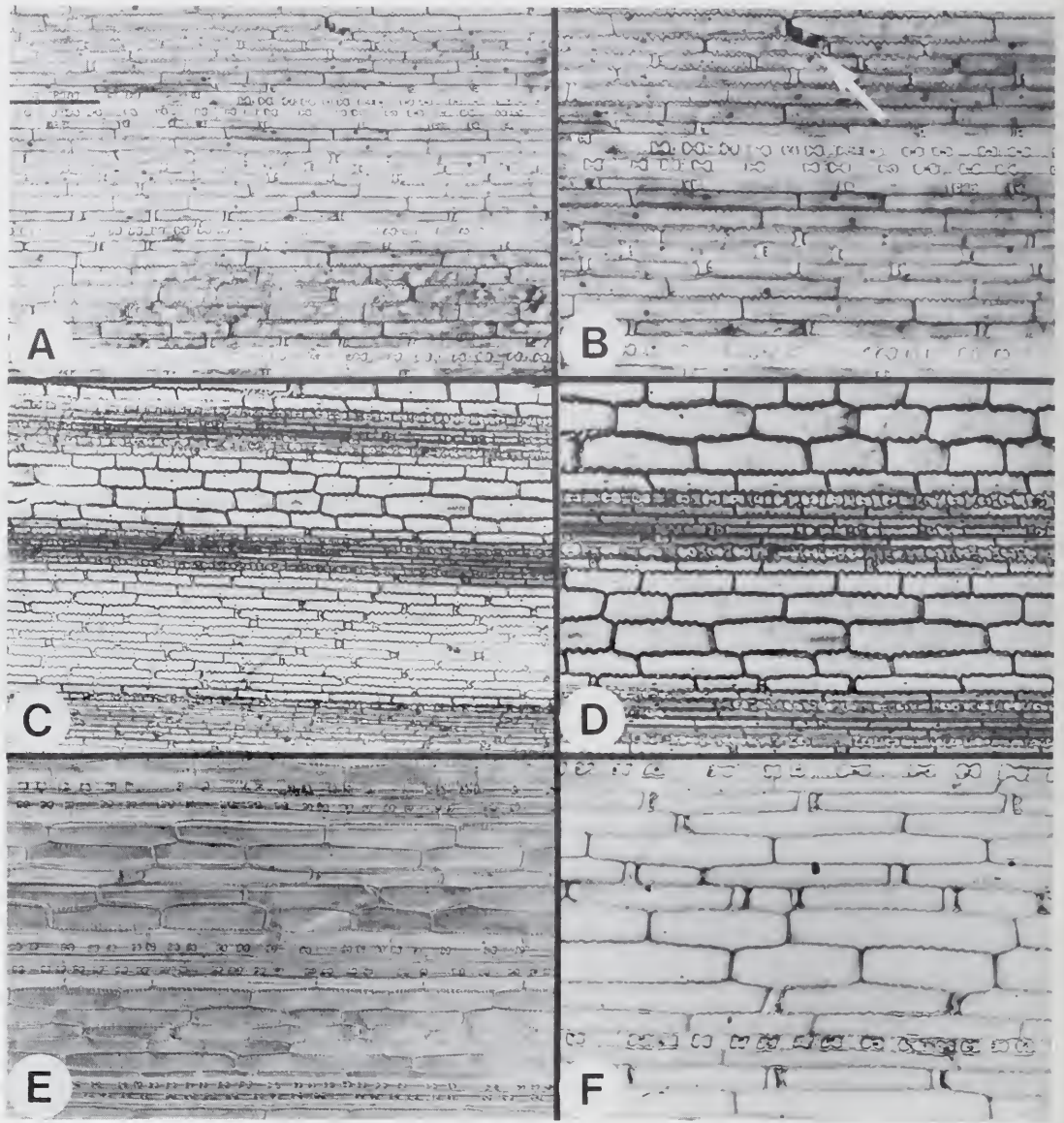


FIGURE 42.2.—*Pentaschistis tortuosa*: abaxial epidermal anatomy.

A, clear distinction between costal and intercostal zones; note complete absence of stomata.

B, costal zones with dumbbell silica bodies whereas those of the intercostal zones are tall, saddle-shaped; note micro-hair (arrowed).

C, zonation showing narrower intercostal long cells adjacent to the median bundle than those more laterally located; these narrower intercostal long cells without papillae.

D, detail of costal silica bodies and short intercostal long cells with thickened, sinuous periclinal walls.

E, interference contrast illumination of costal and intercostal cells.

F, epidermal cell detail with dumbbell-shaped costal silica bodies and tall, narrow intercostal ones.

A, B, *Ellis* 2227; C, D, *Ellis* 5603; E, *Ellis* 2310; F, *Ellis* 2261. A, C, $\times 160$; B, D–F, $\times 250$.

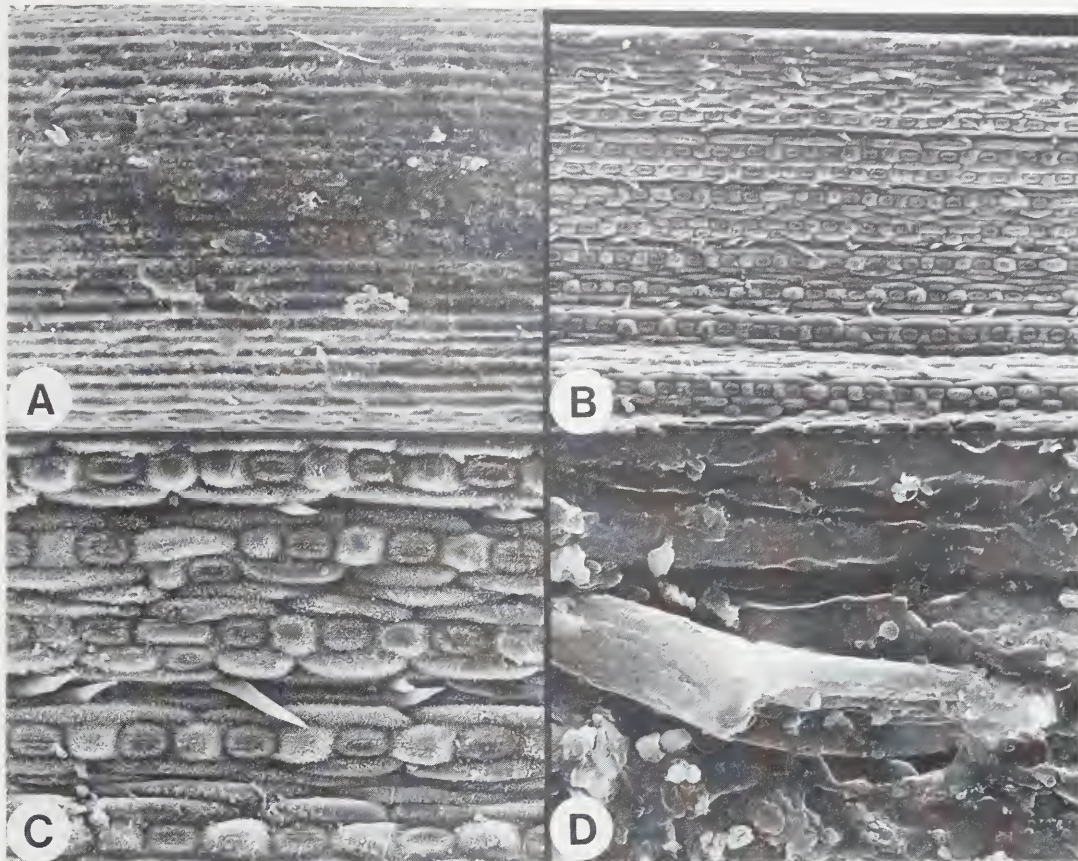


FIGURE 42.3.—*Pentaschistis tortuosa*: SEM of abaxial and adaxial epidermides.

A, featureless abaxial epidermis.

B, adaxial epidermis showing papillate interstomatal cells.

C, more detail of adaxial stomata, papillae and prickles.

D, adaxial microhair with both cells of similar length.

A–D, *Ellis 5603*. A, B, $\times 60$; C, $\times 200$; D, $\times 1000$.

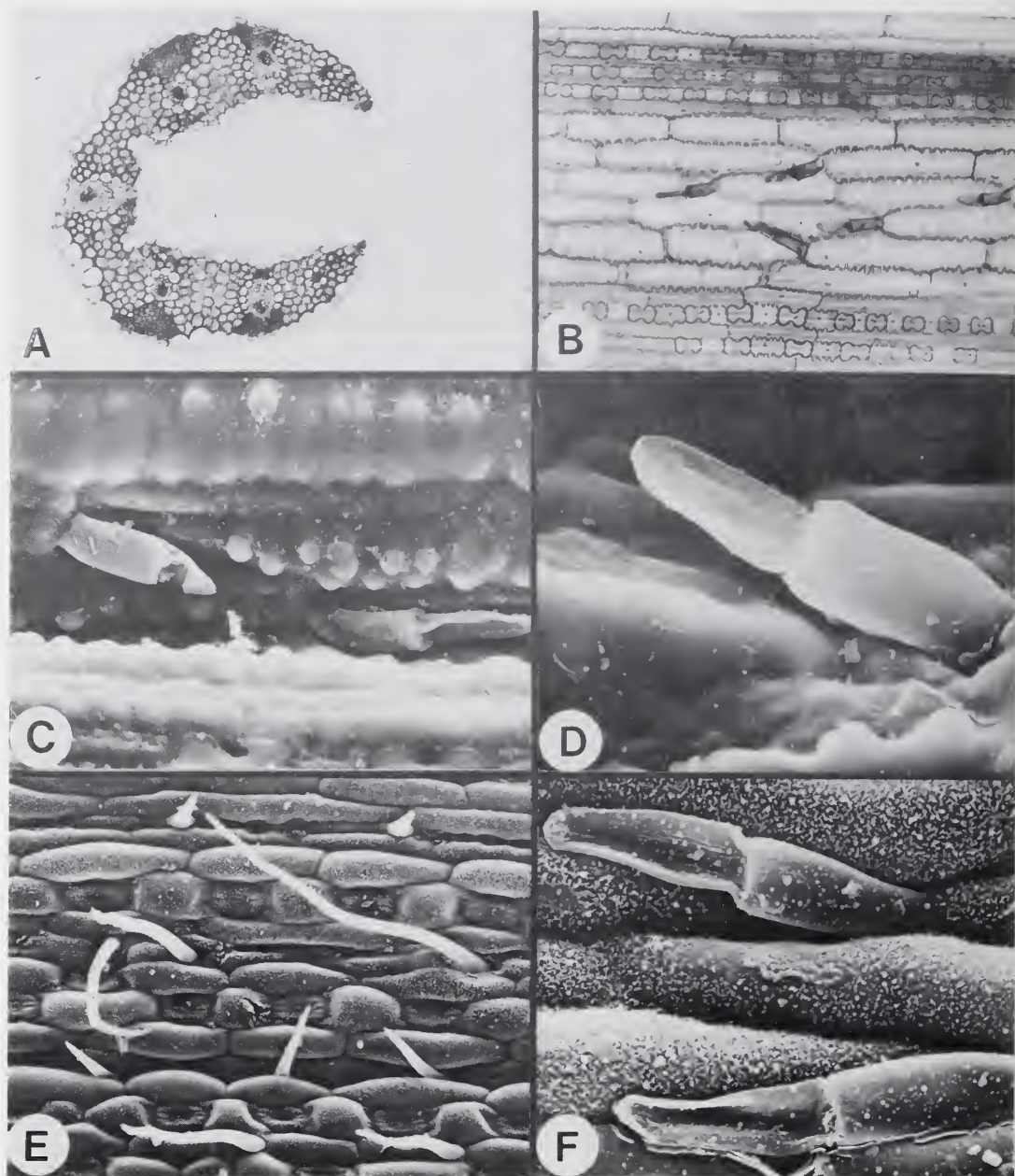


FIGURE 43.1.—*Pentaschistis alticola*: leaf blade anatomy and ultrastructure.

A, very narrow canalliculate leaf outline with only seven vascular bundles; compact mesophyll with vacuolate chlorenchyma cells and large abaxial intercostal epidermal cells.

B, abaxial epidermis with dumbbell-shaped costal silica bodies and intercostal long cells with cuticular papillae; note numerous intercostal microhairs.

C, adaxial epidermis showing cuticular papillae and microhair.

D, detail of abaxial microhair showing relative lengths of basal and distal cells.

E, adaxial surface with inflated, papillate long cells overarched stomata; note prickly hairs which become elongated, resembling macrohairs.

F, adaxial microhairs with distal cells almost as long as basal cells.

A–F, *Ellis* 5528. A, E, $\times 250$; B, C, $\times 400$; D, F, $\times 950$.

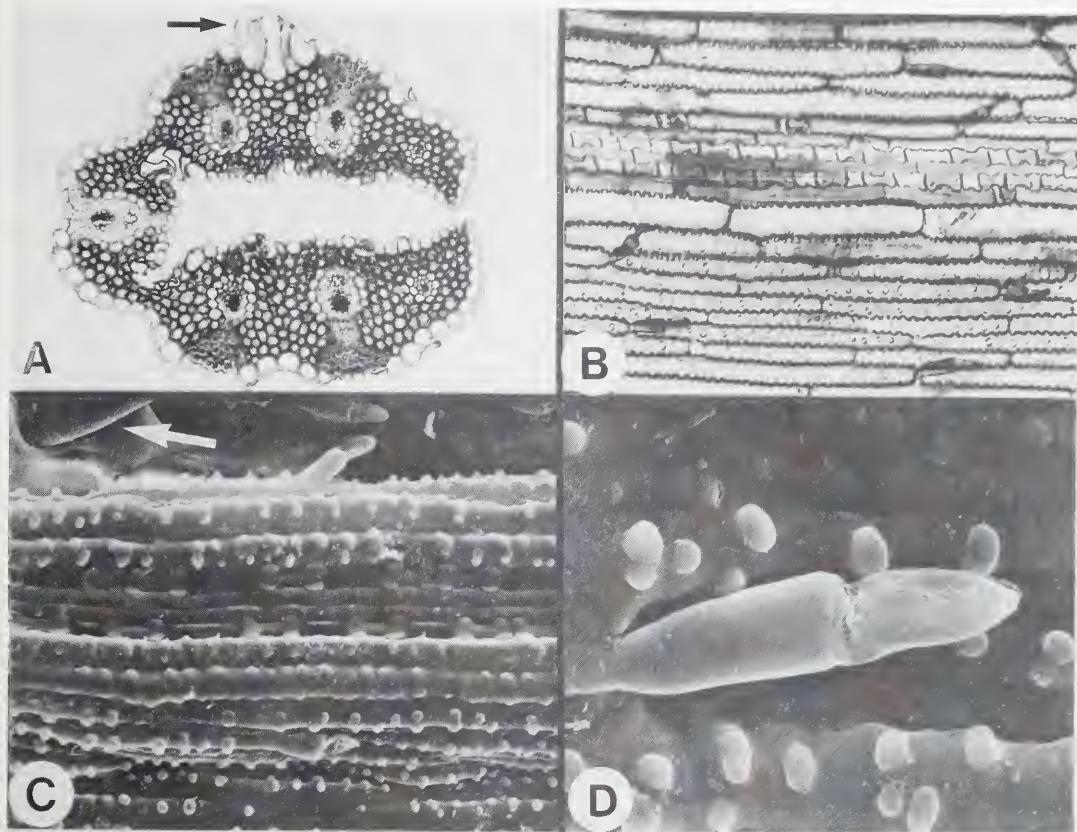


FIGURE 43.2.—*Pentaschistis alticola*: leaf anatomy of specimen with awnless lemmas.
 A, infolded, elliptical outline with typical *P. colorata* type structure; note raised cushion cells of macrohair (arrowed).
 B, abaxial epidermis with elongate, dumbbell-like silica bodies, papillate long cells and microhairs.
 C, papillate abaxial long cells; note microhairs and base of macrohair (arrowed).
 D, detail of cuticular papillae and abaxial microhair.
 A–D, *Ellis 5502*. A, B, $\times 400$; C, $\times 204$; D, $\times 800$.

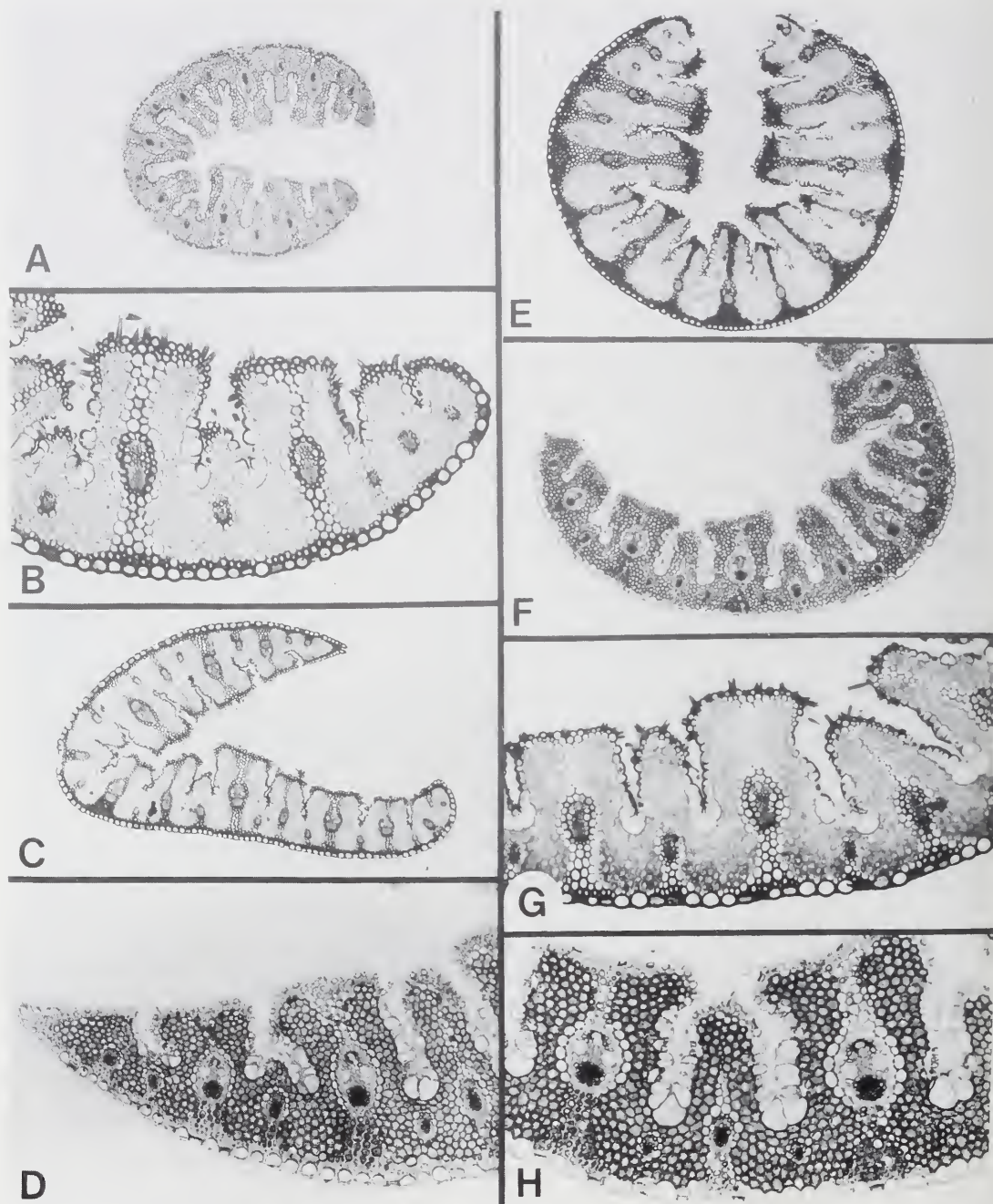


FIGURE 44.1.—*Pentaschistis pyrophila*: leaf blade in transverse section.

A, setaceous leaf blade in which the laminae are symmetrical.

B, detail showing continuous abaxial hypodermal sclerenchyma layer only linked to the larger bundles by collenchyma tissue; note difference in size between adaxial ribs overlying first and third order bundles; adaxial prickles on the tops of the ribs; chlorenchyma of tightly packed angular cells.

C, rather wide, infolded leaf blade in which the two halves of the lamina are asymmetrical with the median bundle being located off-centre; note sequence of arrangement of the vascular bundles which are of three size classes.

D, sharply tapering margin, massive adaxial ribs and cleft-like furrows, hypodermal sclerenchyma, abaxial epidermal cells of uniform size throughout epidermis and larger than the adaxial epidermal cells and compact chlorenchyma.

E, acicular, permanently infolded blade with lignified secondary cell walls.

F, wide, inrolled blade illustrating the vascular bundle sequence of 1st, 3rd, 2nd, 3rd, 1st repeated across the leaf width.

G, typical cross sectional structure showing black lignified tissue; note bundle sheath extensions intergrading into abaxial hypodermal layer.

H, detail of chlorenchyma tissue and differences between 1st, 2nd and 3rd order vascular bundles.

A, B, Ellis 5626; C, D, Ellis 5618; E, Ellis 5530; F, H, Ellis 5556; G, Ellis 5623. A, C, E, F, $\times 100$; B, D, G, H, $\times 250$.

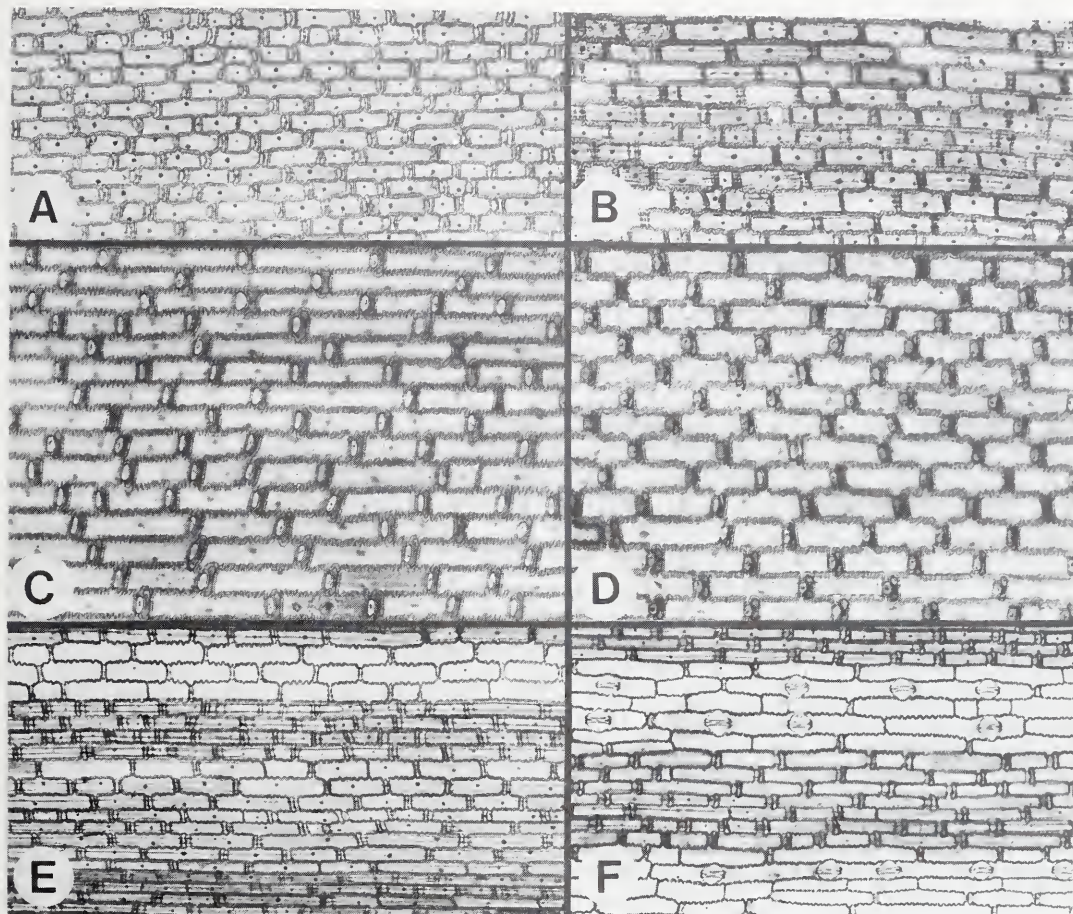


FIGURE 44.2.—*Pentaschistis pyrophila*: abaxial epidermal structure.

A, no zonation evident with short, thick-walled, nucleate long cells always separated by tall and narrow cork-silica cell pairs; no epidermal appendages or stomata.

B, typical brick-work pattern of epidermal cell arrangement; long cells nucleate.

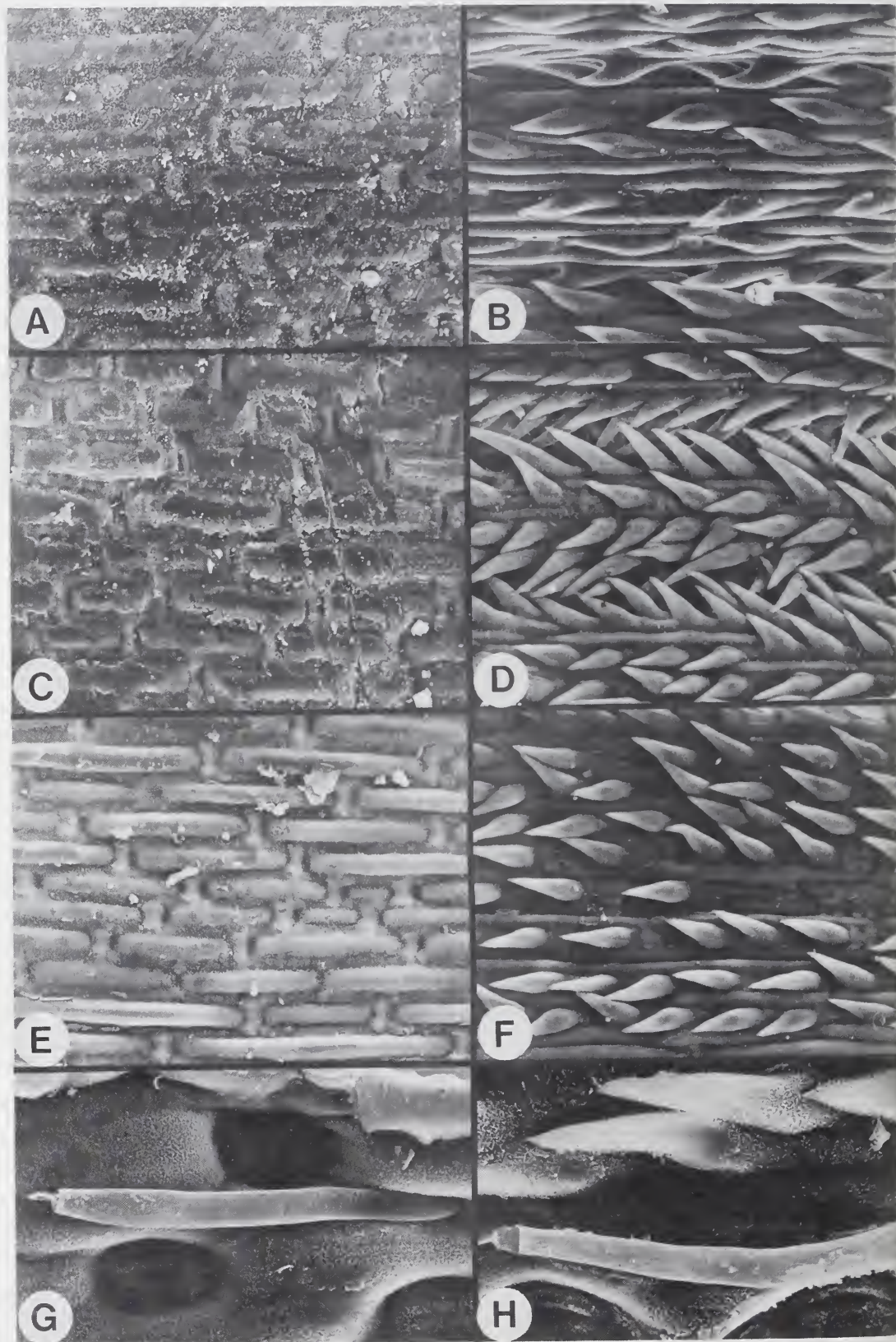
C, rectangular long cells with thick sinuous anticlinal walls, cork-silica pairs with tall and narrow cork cell enfolding elliptical silica body.

D, typical epidermis without zonation, stomata or appendages.

E, slightly atypical specimen with signs of zonation evident; no stomata.

F, unusual specimen with abaxial stomata; these stomata visible in transverse section (Figure 44.1H); abaxial micro-hairs not present.

A, *Ellis* 5626; B, *Ellis* 5618; C, *Ellis* 5530; D, *Ellis* 5533; E, *Ellis* 5623; F, *Ellis* 5556. A–F, $\times 250$.



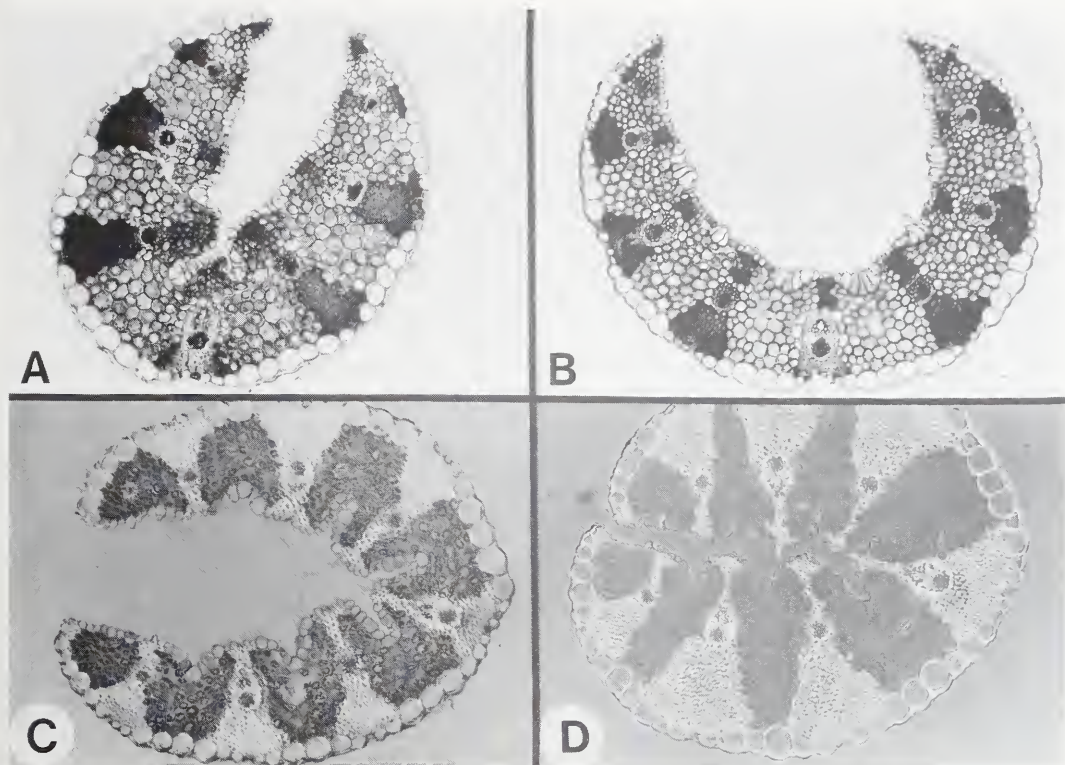


FIGURE 45a.1—*Pentaschistis calcicola* var. *calcicola*: transectional leaf anatomy.

A, tightly infolded setaceous outline; note compact mesophyll and large intercostal long cells.
 B, wider, more open inrolled leaf; note sclerenchyma girders and few adaxial macrohairs in section.
 C, interference contrast of transverse section of blade clearly showing extent of girder development.
 D, interference contrast of thick, permanently inrolled blade with massive abaxial girders.
 A, *Ellis* 5449; B, *Ellis* 5447; C, *Ellis* 1667; D, *Ellis* 1282. All $\times 250$.

FIGURE 44.3.—*Pentaschistis pyrophila*: epidermal ultrastructure.

A, featureless abaxial epidermal surface.
 B, adaxial ribs with numerous prickly hairs.
 C, brickwork pattern of long cell arrangement.
 D, dense adaxial prickles overarching cleft-like furrows.
 E, abaxial long and short cells; note absence of stomata which were present on another leaf viewed under light microscopy (Figure 44.2F).
 F, diagnostic adaxial prickles.
 G, very thin, elongated adaxial microhair with minute distal cell.
 H, long, slender microhair with minute distal cell.
 A, B, *Ellis* 5530; C, D, H, *Ellis* 5618; E–G, *Ellis* 5556. A–F, $\times 200$; G, $\times 500$; H, $\times 600$.

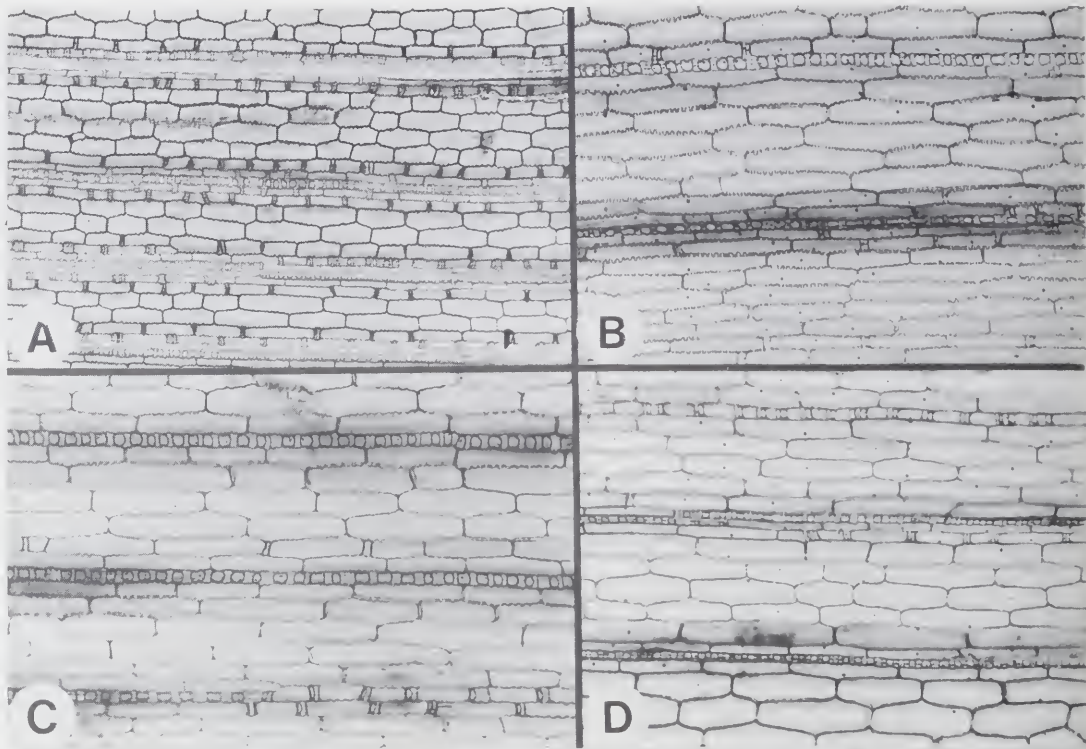


FIGURE 45a.2—*Pentaschistis calcicola* var. *calcicola*: abaxial epidermis with no stomata or macrohairs.
 A, epidermal zonation with short, fusiform long cells, no stomata and microhairs; costal zones narrow despite very wide abaxial girders.
 B, very irregularly shaped silica bodies, with few tending to dumbbell type; sinuous fusiform long cells.
 C, typical epidermal zonation; note irregularly dumbbell-shaped silica bodies.
 D, typical abaxial epidermal structure; note nuclei in long cells.
 A, Ellis 2511; B, Ellis 5448; C, Ellis 1282; D, Ellis 5447. A, $\times 160$; B–D, $\times 250$.

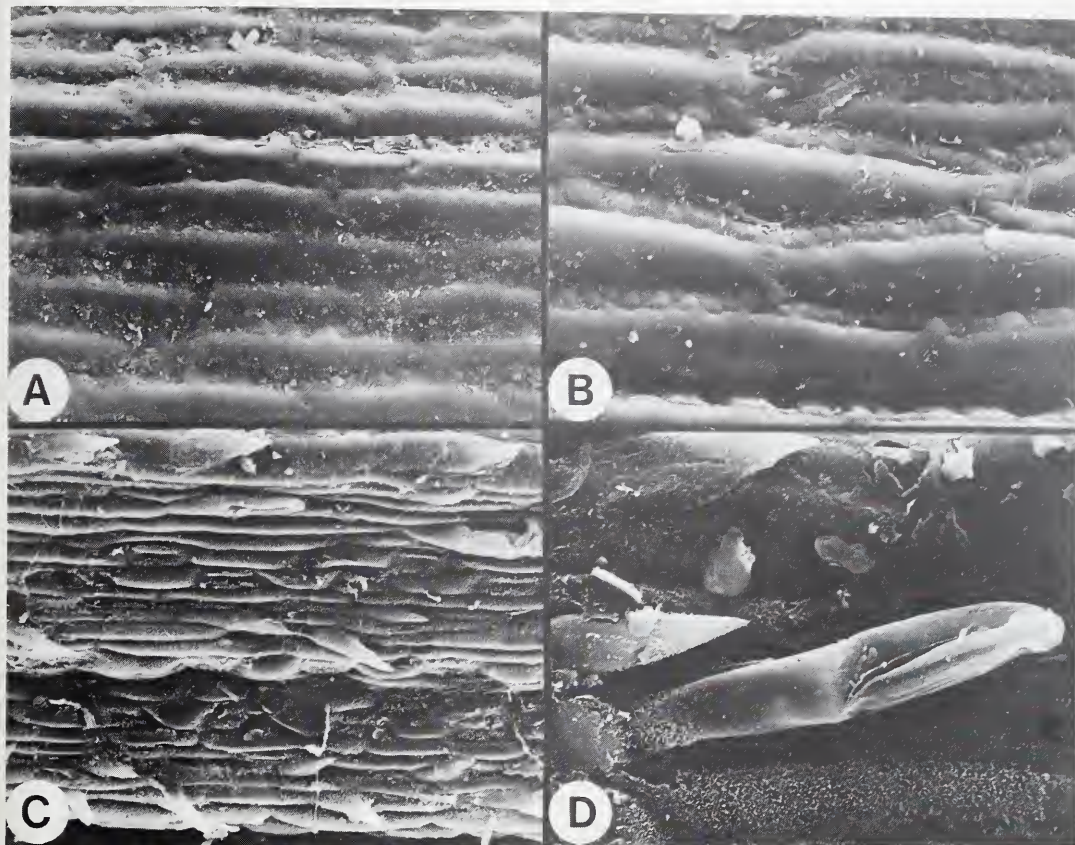


FIGURE 45a.3.—*Pentaschistis calcicola* var. *calcicola*: SEM of leaf epidermides. A, B, abaxial epidermis. C, D, adaxial epidermis.

A, featureless surface with only intercostal long cells visible.

B, detail of thickened, sinuous long cell walls.

C, inflated adaxial long cells and few prickles and microhairs.

D, prickle and microhair with basal and distal cells about equal in length.

A, *Ellis 5449*; B, C, D, *Ellis 5447*. A, C, $\times 200$; B, $\times 350$; D, $\times 700$.

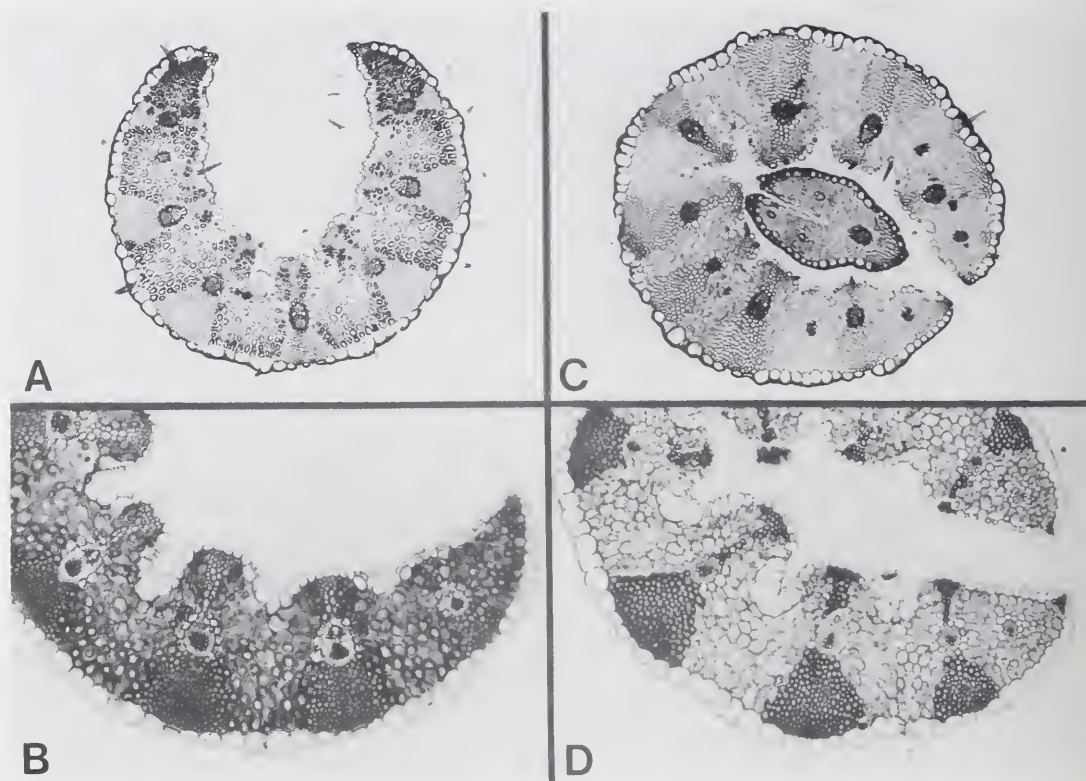


FIGURE 45b.1.—*Pentaschistis calcicola* var. *hirsuta*: leaf blade in cross section.

A, infolded blade with many macrohairs on both surfaces.

B, detail showing compact mesophyll, girders, chloroplasts in bundle sheath cells and large abaxial epidermal cells with superficial macrohairs; note secondary thickening not lignified.

C, leaf blade enfolding developing leaf; note girders are not lignified as they do not stain darkly.

D, detail of rather compact mesophyll and massive abaxial girders associated with all vascular bundles.

A, B, *Ellis* 2530; C, *Ellis* 5451; D, *Ellis* 5149. A, C, $\times 160$; B, D, $\times 250$.

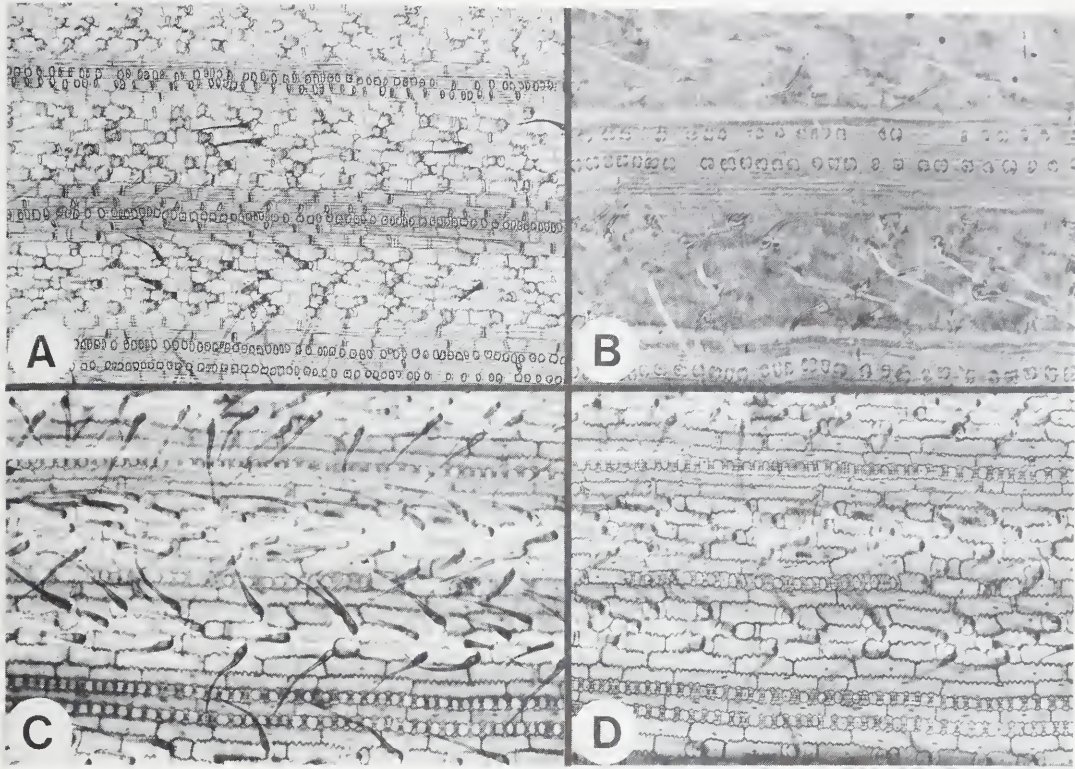


FIGURE 45b.2.—*Pentaschistis calcicola* var. *hirsuta*: puberulous abaxial epidermis.

A, epidermal pattern with costal and intercostal zones, no stomata and intercostal macrohairs very common; note very irregular silica bodies, only a few tending to the dumbbell shape.

B, interference contrast showing short macrohairs with slightly swollen superficial bases and irregular dumbbell-shaped silica bodies.

C, detail of macrohairs showing swollen bases.

D, same field but different focus to C with inflated epidermal cell associated with the macrohair bases clearly visible.

A, *Ellis* 2530; A, *Ellis* 1654; C, D, *Ellis* 5451. A, $\times 160$; B–D, $\times 250$.

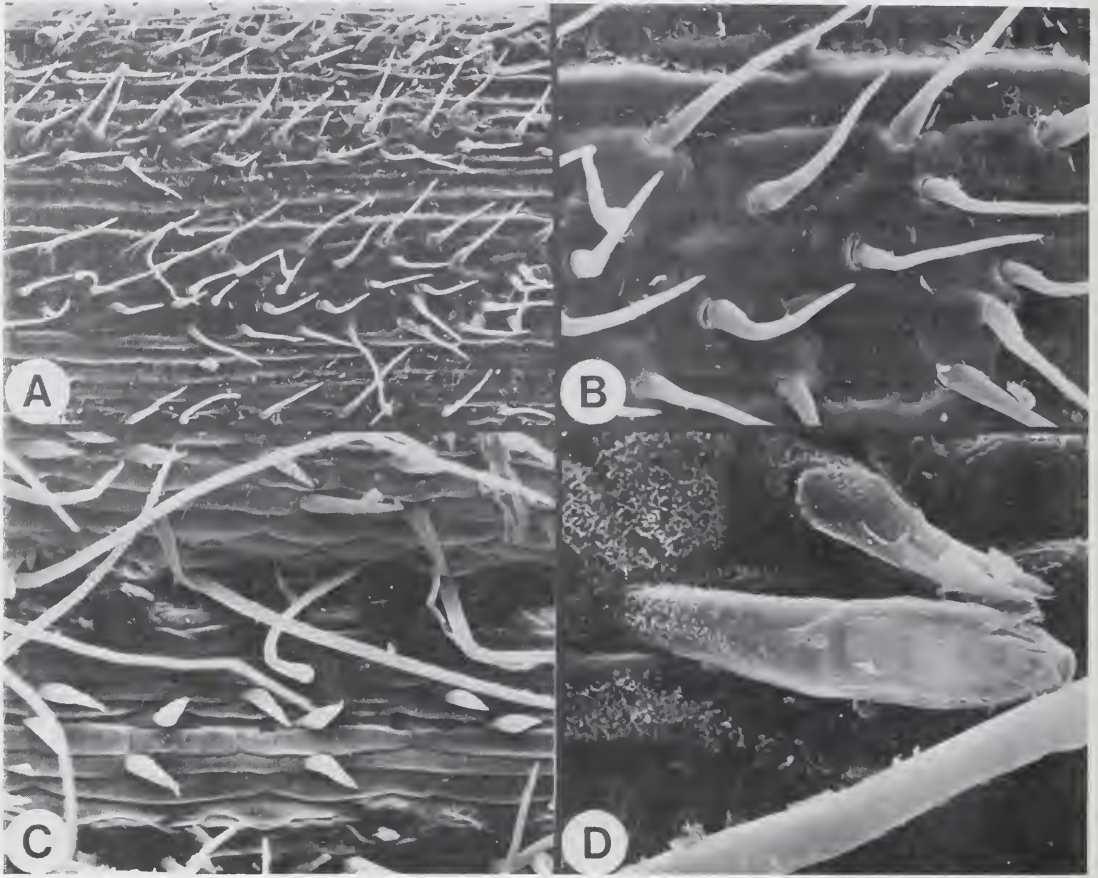


FIGURE 45b.3.—*Pentaschistis calcicola* var. *hirsuta*: epidermal ultrastructure. A, B, abaxial epidermis. C, D, adaxial epidermis.

A, dense indumentum of intercostal macrohairs.

B, detail of macrohairs with swollen bases not inserted in raised cushions; note absence of stomata.

C, adaxial surface with longer macrohairs and short costal prickles.

D, adaxial microhair with distal cell longer than basal cell; note prickle and macrohair and epicuticular wax.

A, B, D, *Ellis 5451*; C, *Ellis 5149*. A, $\times 60$; B, C, $\times 200$; D, $\times 1100$.

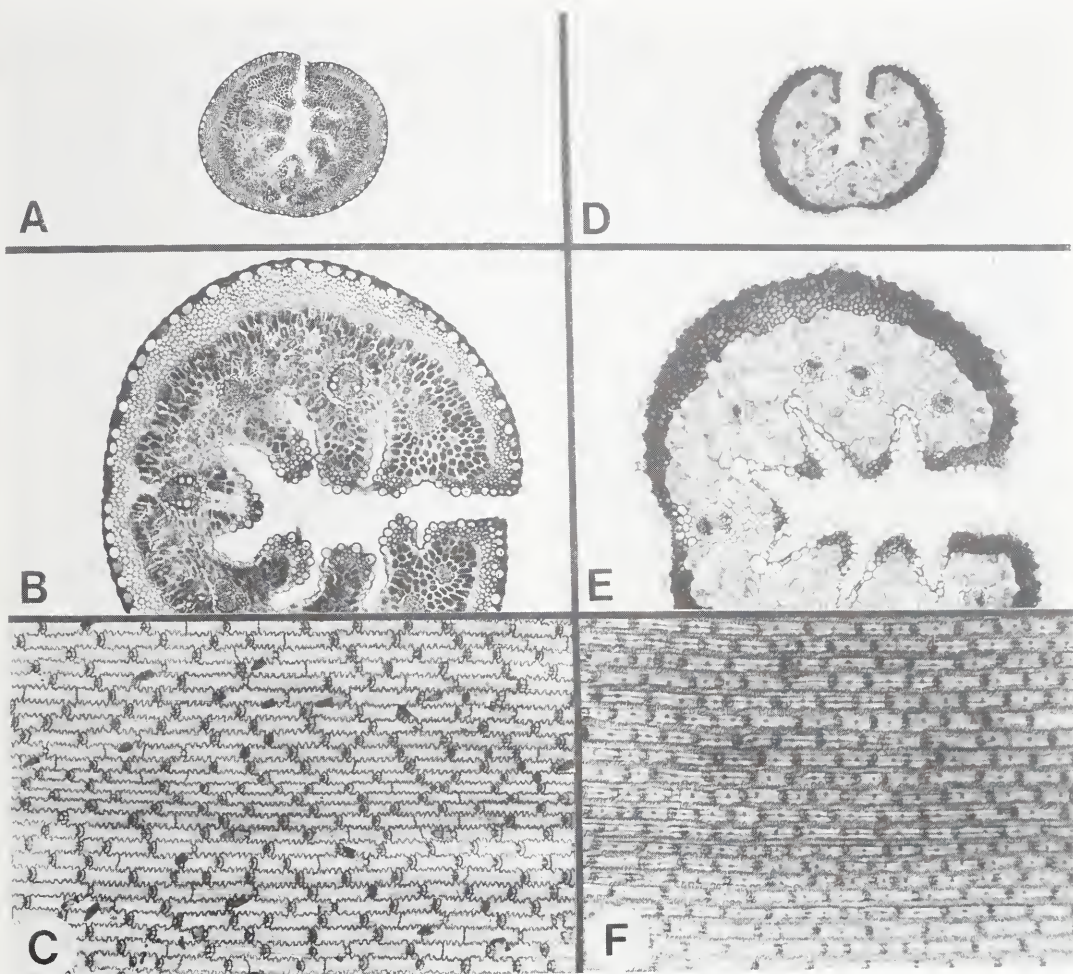


FIGURE 46.1.—*Pentaschistis montana*: leaf blade anatomy.

A, tightly inrolled leaf with narrow adaxial channel.

B, anatomical detail showing the wide, continuous hypodermal band adjacent to the abaxial epidermis; this sclerenchyma tissue is not linked to the vascular bundles by girders; the chlorenchyma is not of the sclerophyllous type but consists of irregularly shaped cells diffusely arranged.

C, abaxial epidermis without zonation or stomata; shortly rectangular long cells with sinuous walls alternate with cork-silica pairs (with cork cell enfolding smaller silica cell) along all files; note high frequency of occurrence of microhairs which are relatively broad with basal and distal cells more or less equal in length.

D, setaceous outline clearly showing hypodermal fibrous tissue.

E, detail of thick, continuous hypodermal layer, absence of girders and mesic type mesophyll.

F, abaxial epidermis with very thick and sinuous anticlinal long cell walls; each long cell alternates with much narrower cork-silica cell pair; few microhairs visible.

A–C, Ellis 2479; D–F, Linder 4413. A, D, $\times 100$; B, C, E, F, $\times 250$.

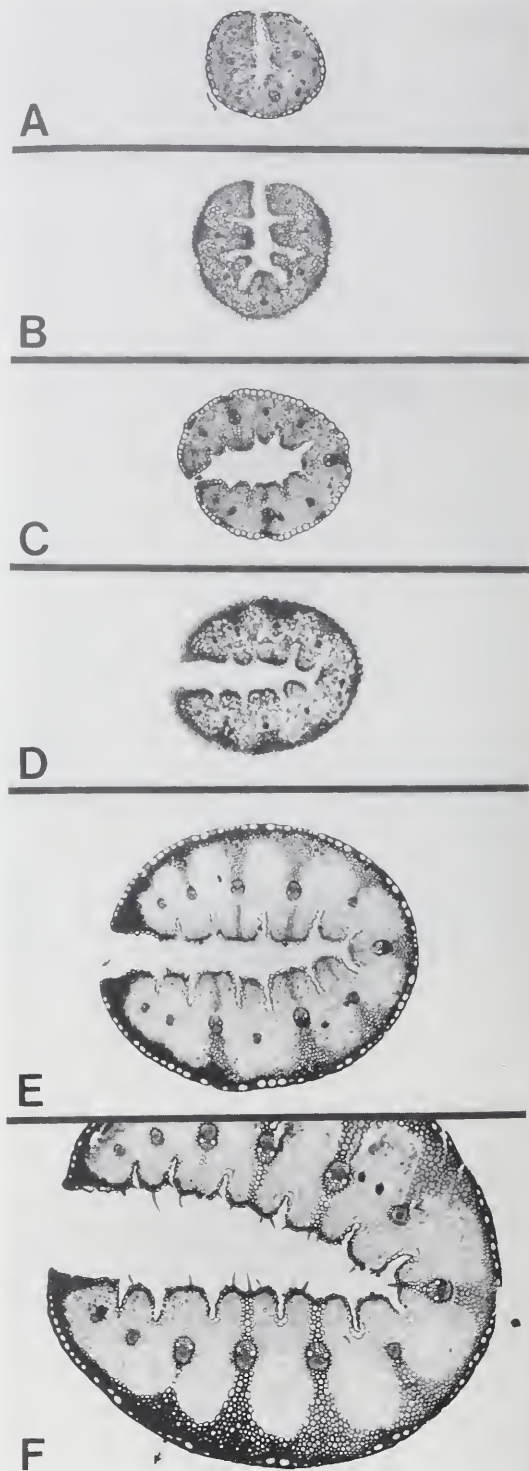


FIGURE 47.1.—*Pentaschistis rigidissima*: variation in size and shape of leaf outline.

A, very narrow, rounded leaf with narrow adaxial channel; 7 bundles in blade.

B, narrow, inrolled blade with prominent adaxial ribs and furrows; 7 bundles in blade.

C, narrow leaf with canaliculate adaxial channel; slightly wider than A and B with 9 bundles in blade.

D, setaceous blade with 9 bundles.

E, wider permanently infolded blade with 11 bundles.

F, wide setaceous blade with 13 vascular bundles.

A, *Ellis 5619*; B, *Ellis 5606*; C, *Ellis 5612*; D, *Ellis 5531*; E, *Ellis 5624*; F, *Ellis 5813*. A–F, $\times 100$.

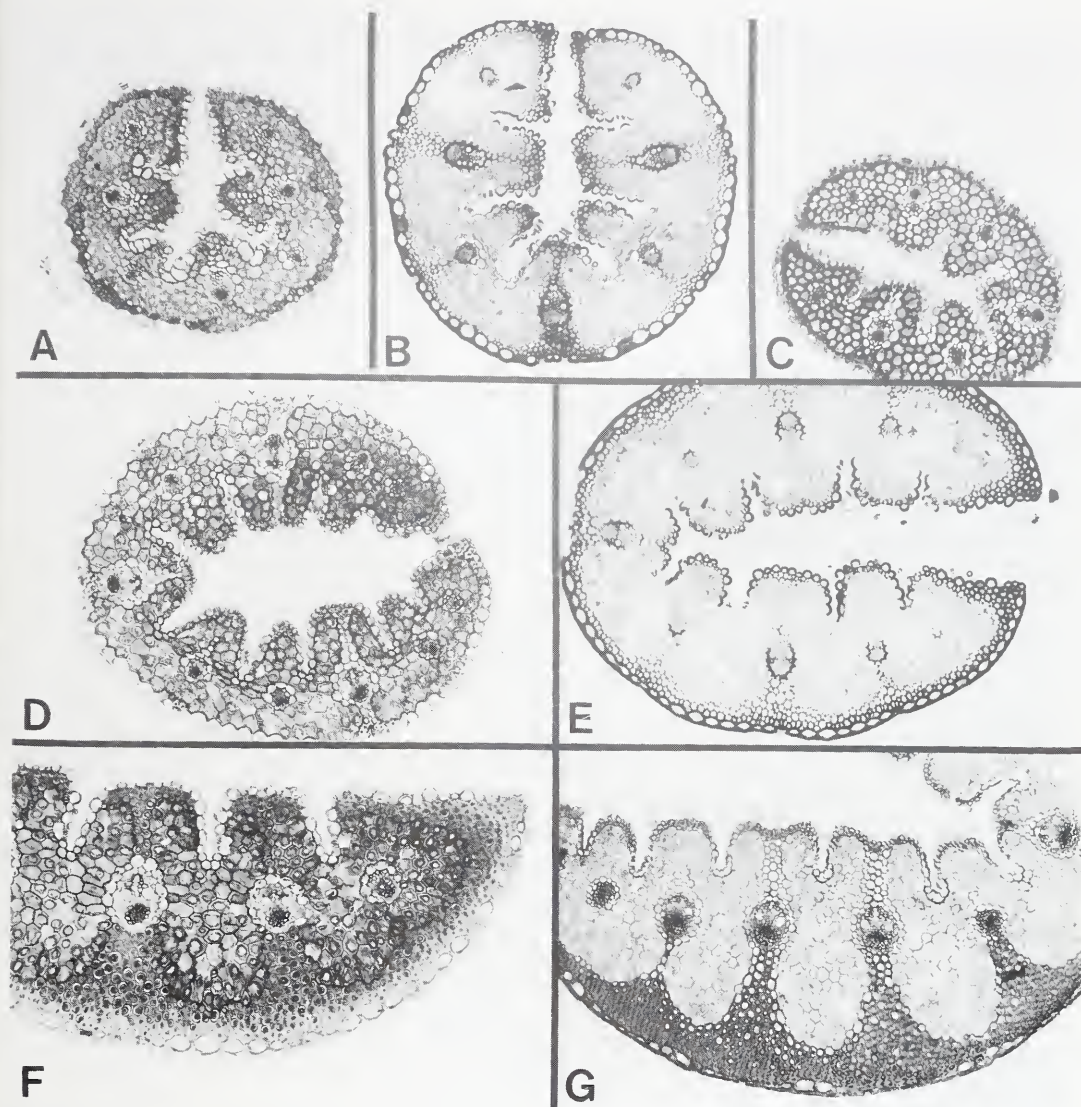


FIGURE 47.2.—*Pentaschistis rigidissima*: detail of transectional anatomy.

A, large, thickened abaxial epidermal cells; continuous hypodermal sclerenchyma, not linked to bundles by abaxial girders; alternating first and third order vascular bundles; rather dense, compact chlorenchyma of angular cells.

B, similar structure to A but leaf slightly wider; note chlorenchyma less regular, particularly at bases of adaxial furrows.

C, large abaxial epidermal cells with thick cuticle, thin hypodermal layer but chlorenchyma cells relatively large—similar in size to outer bundle sheath cells; note canaliculate tendency of adaxial channel.

D, canaliculate adaxial channel; note large chlorenchyma cells and absence of abaxial hypodermal layer.

E, lignified tissue darkly stained; note diffuse nature of mesophyll.

F, massive trapezoidal abaxial girders fused laterally; note size of chlorenchyma cells in relation to bundle sheath cells; mesophyll tissue relatively compact but air spaces visible.

G, lignified abaxial sclerenchyma girders fused to form continuous hypodermal layer; mesophyll tissue rather diffuse with intercellular air spaces evident; note sequence of vascular bundles with lateral first order bundles adjacent to one another.

A, Ellis 5619; B, Ellis 5606; C, Ellis 5585; D, Ellis 5612; E, Ellis 5531; F, Ellis 2558; G, Ellis 5813. A–G, $\times 250$.

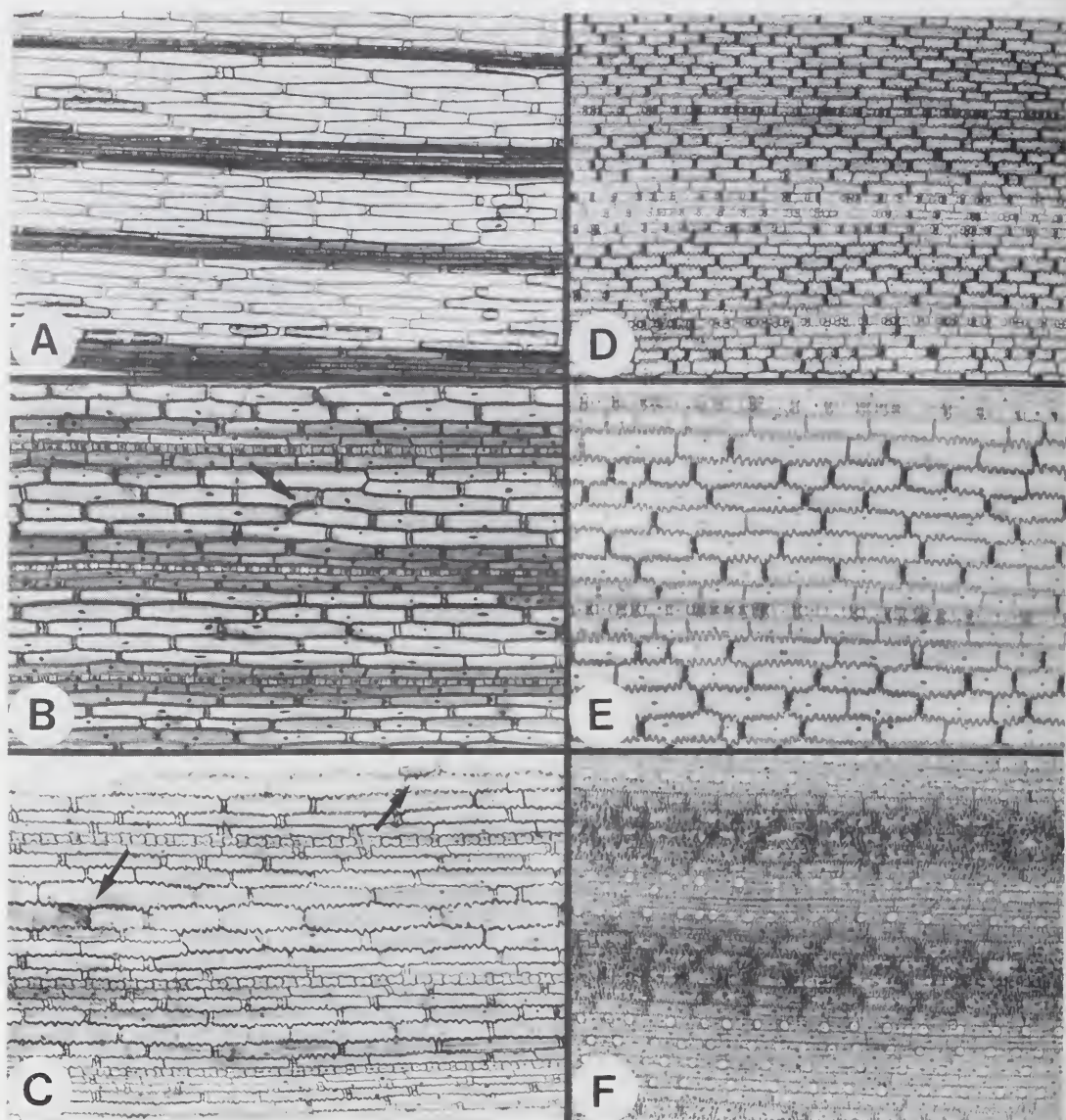


FIGURE 47.3.—*Pentaschistis rigidissima*: variation in abaxial epidermal structure. A–C, specimens displaying epidermal zonation. D–F, specimens without epidermal zonation.

A, distinct costal and intercostal zones with elongated fusiform long cells with very slightly sinuous walls; no microhairs; specimen without hypodermal sclerenchyma layer.

B, zonation developed but long cells shorter and more sinuous than A; note minute angular costal silica bodies; microhairs common (arrowed).

C, costal zones with dumbbell-shaped silica bodies, intercostal long cells with moderately sinuous walls and microhairs present (arrowed).

D, zonation indistinct and intercostal long cells very short; no microhairs.

E, short, rectangular intercostal long cells with very sinuous walls, alternating with tall cork cells; costal files very narrow with silica bodies irregular in shape and arrangement; note nucleate long cells and absence of microhairs.

F, short intercostal long cells with very sinuous and pitted anticlinal walls; wide costal zones with round silica bodies in alternating files.

A, Ellis 5612; B, Ellis 5611; C, Ellis 5606; D, Ellis 5534; E, Ellis 5625; F, Ellis 5813. A, D, $\times 160$; B, C, E, F, $\times 250$.

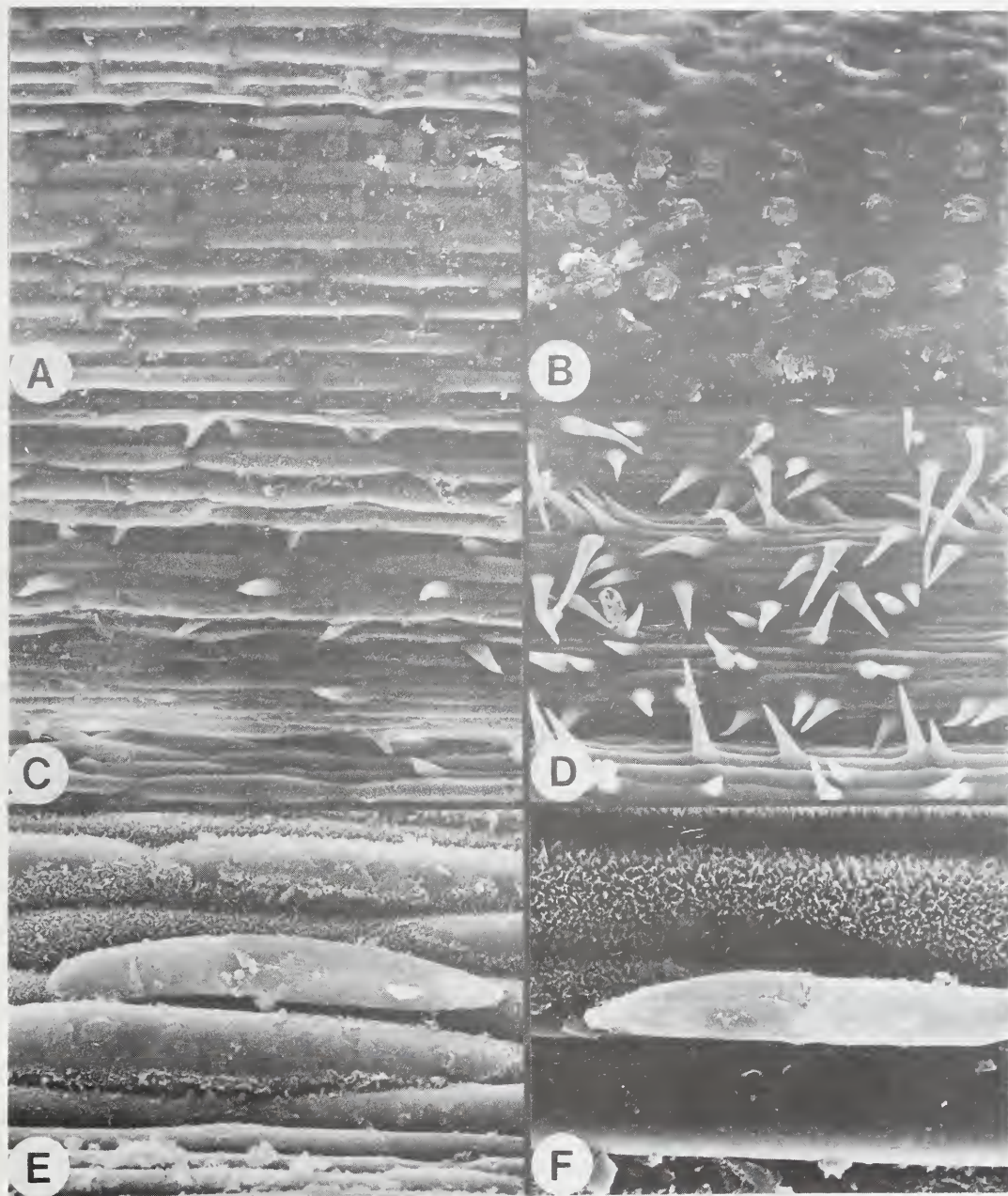


FIGURE 47.4.—*Pentaschistis rigidissima*: leaf blade ultrastructure. A, B, abaxial epidermis. C–F, adaxial epidermis. A, long cells with thick anticlinal walls and raised periclinal walls; round silica bodies; no stomata or appendages. B, raised, rounded silica bodies on leaf with very thick cuticle. C, adaxial ribs without inflated long cells; few small prickles present. D, adaxial ribs with elongate prickly hairs. E, adaxial microhair with tapering distal cell longer than basal cell. F, microhair with distal and basal cells equal in length. A, C, E, *Ellis* 5622; B, D, *Ellis* 5813; F, *Ellis* 5518. A–D, $\times 200$; E, $\times 670$; F, $\times 900$.

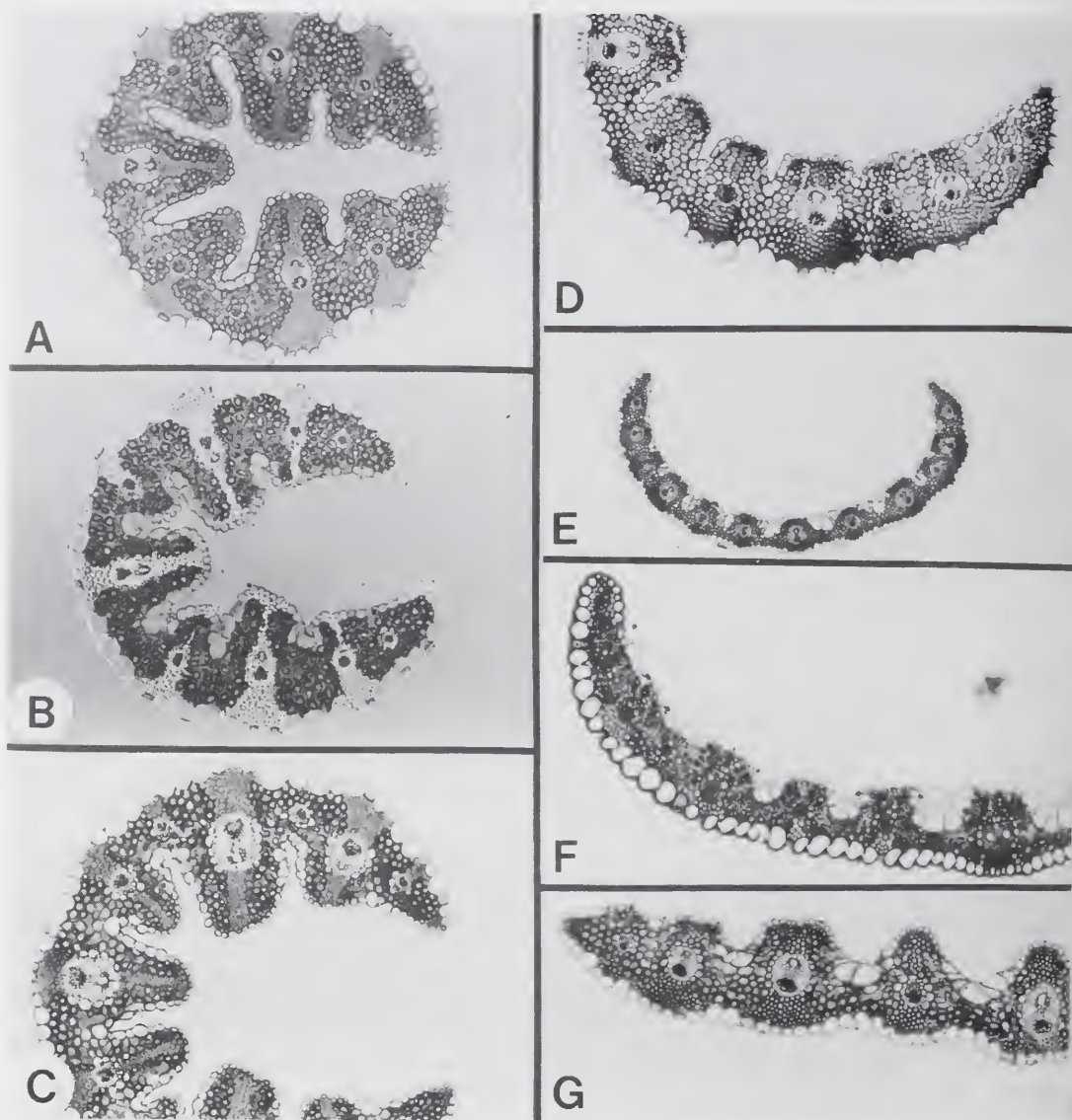


FIGURE 48.1.—*Pentaschistis malouinensis*: transsectional leaf anatomy with variable leaf blade outlines.

A, circular, permanently infolded outline; note adaxial ribs and deep furrows and wide abaxial girders.

B, interference contrast of setaceous leaf; note large abaxial epidermal cells.

C, compact, vacuolate chlorenchyma, girders and colourless bundle sheath cells.

D, margin showing alternating first and third order bundles; note decreasing size of adaxial ribs.

E, open, more expanded leaf blade.

F, thin lamina with large abaxial epidermal cells.

G, unusual abaxial ribs and furrows present.

A, *Ellis* 2345; B, *Ellis* 2346; C, *Ellis* 2538; D, *Ellis* 5542; E, *Ellis* 5503; F, *Ellis* 5613; G, *Ellis* 5153. E, $\times 100$.

A–D, F, G, $\times 250$.

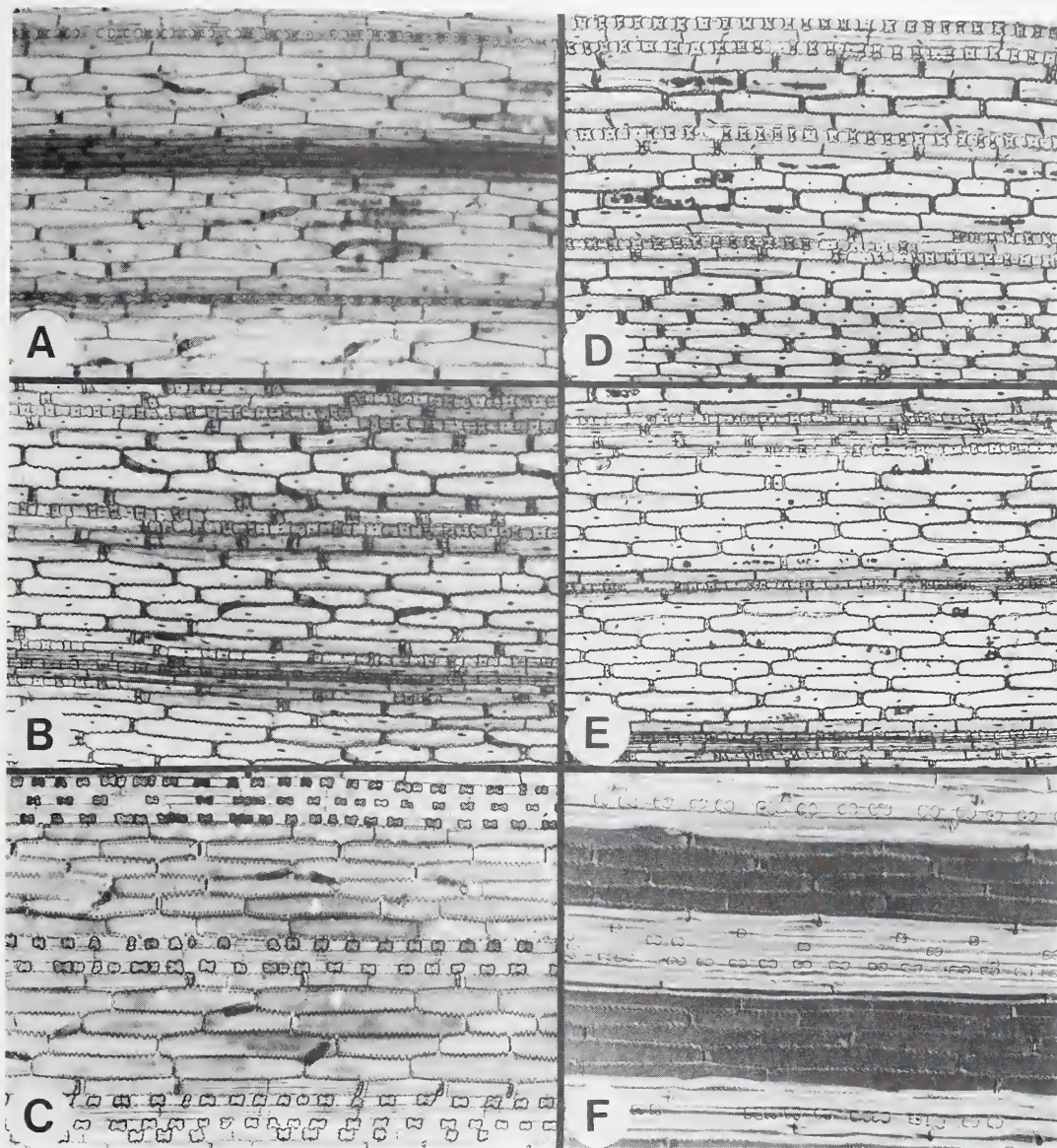


FIGURE 48.2.—*Pentaschistis malouinensis*: uniform abaxial epidermal anatomy without stomata.

A, costal and intercostal zones; note absence of stomata and microhairs with short basal cells.

B, silica bodies, microhairs and nucleate long cells.

C, irregular dumbbell silica bodies, basal cells of microhairs and fusiform long cells with sinuous walls.

D, typical epidermal configuration except no microhairs present.

E, irregular dumbbell-shaped silica bodies, sinuous long cells but no microhairs.

F, interference contrast of costal and intercostal zones.

A, Ellis 5542; B, Linder 4432; C, Ellis 2345; D, Ellis 5583; E, Ellis 5503; F, Ellis 2538. All $\times 250$.

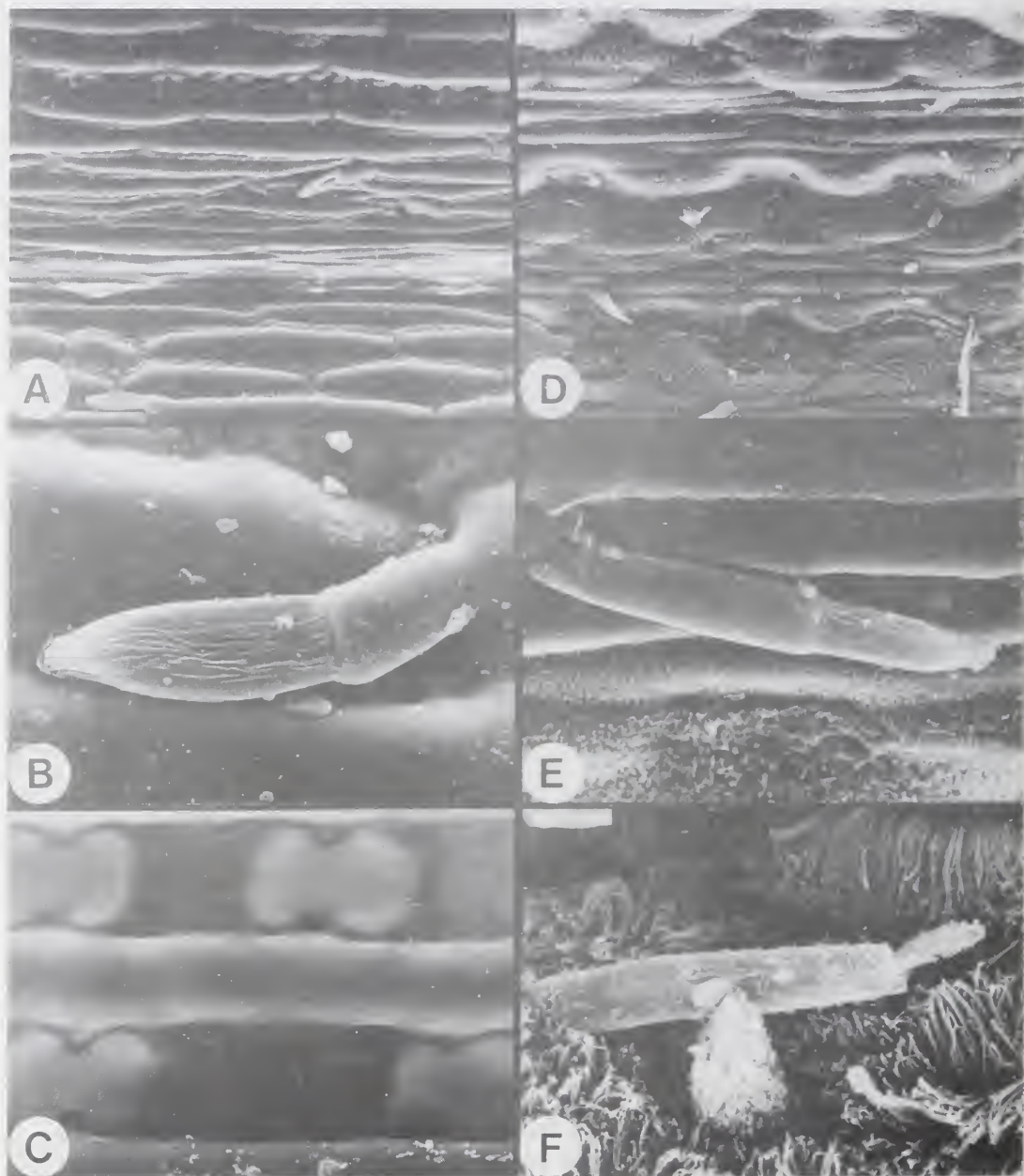


FIGURE 48.3.—*Pentaschistis malouinensis*: epidermal ultrastructure. A–C, abaxial epidermis. D–F, adaxial epidermis.

A, fusiform long cells with slightly inflated periclinal walls; note microhairs.

B, microhair with longer distal cell than basal cell.

C, costal zone showing dumbbell-shaped silica bodies.

D, slightly inflated long cells, sunken stomata.

E, adaxial microhair more slender than those on abaxial surface.

F, adaxial microhair from high altitude specimen; note wax rods.

A, B, *Ellis 5542*; C–E, *Ellis 5583*; F, *Ellis 5613*. A, D, $\times 200$; E, $\times 800$; B, $\times 850$; C, F, $\times 1000$.

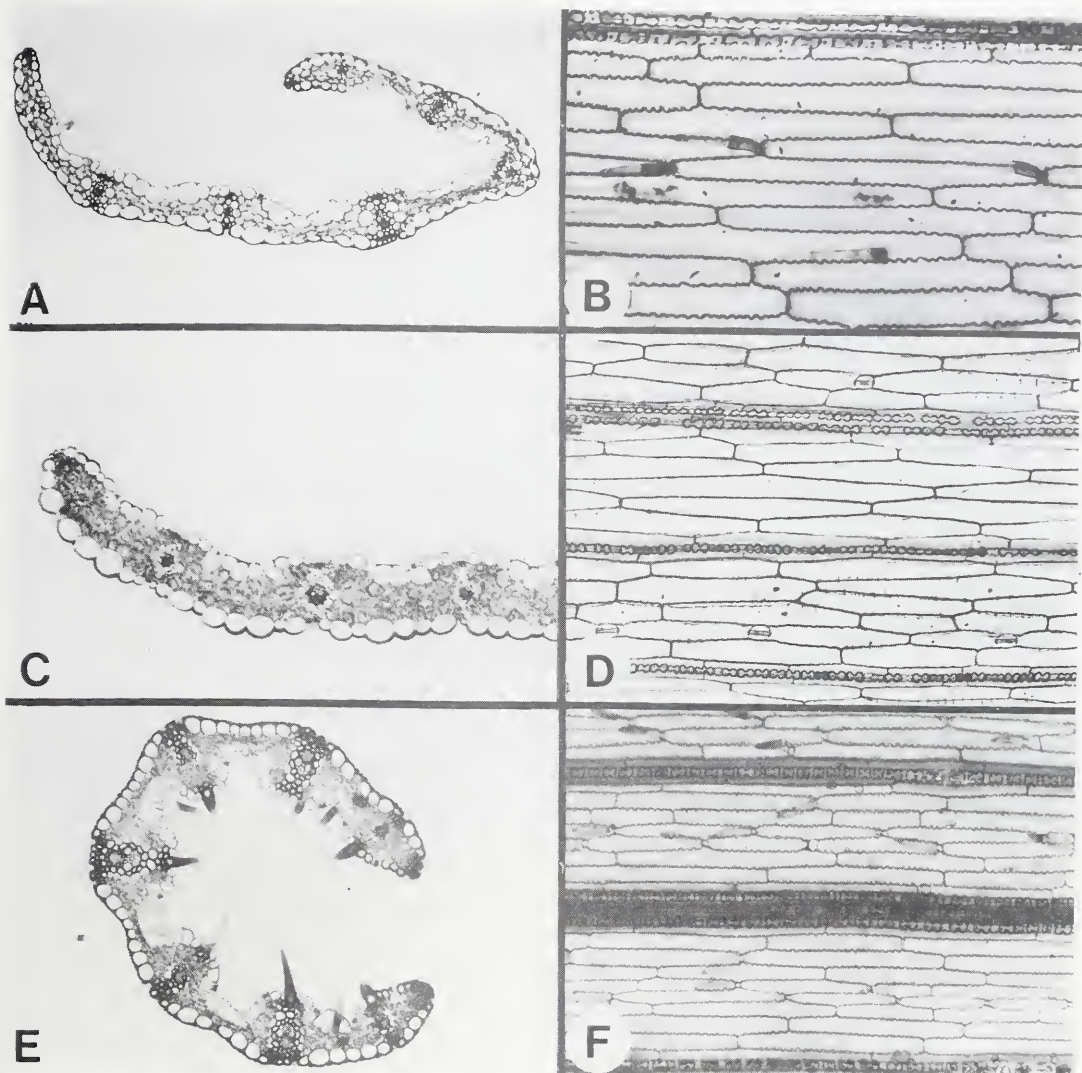


FIGURE 49.1.—*Pentaschistis pusilla*: leaf anatomy. A, C, E, transectional anatomy. B, D, F, abaxial epidermis. A, very thin but expanded blade; note wide bulliform fans and mesic type mesophyll.

B, abaxial epidermis with wide intercostal zones with fusiform long cells, no stomata and microhairs with shorter basal cells; narrow costal zones with dumbbell-shaped silica bodies.

C, expanded blade with mesic mesophyll, very small sclerenchyma strands, first order bundles separated by two small bundles and large inflated abaxial epidermal cells.

D, abaxial epidermis with fusiform long cells, a few stomata, no microhairs and dumbbell to nodular silica bodies.

E, specimen with narrower leaf resembling that of *P. colorata*—abaxial papillae on either side of median vascular bundle, intercostal long cells larger than costal ones, compact mesophyll and papillate adaxial epidermis; note macrohairs.

F, abaxial epidermis of E with dumbbell silica bodies and microhairs with short basal cells, typical of those of *P. colorata*.

A, B, Ellis 5590; C, D, Ellis 2481; E, F, Esterhuysen 22775. A, D–F, $\times 250$; B, C, $\times 400$.

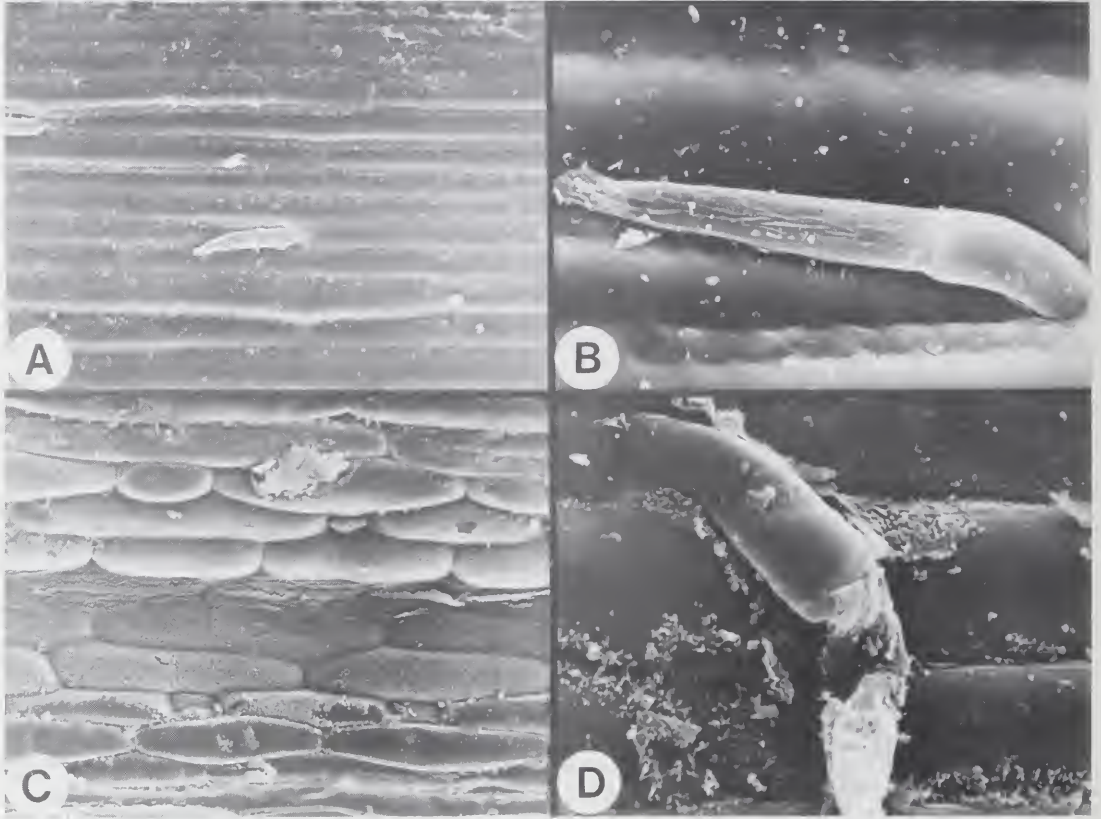


FIGURE 49.2.—*Pentaschistis pusilla*: ultrastructure of leaf blade. A, B, abaxial epidermis. C, D, adaxial epidermis. A, elongate long cells and microhairs. B, microhair with very elongated distal cell. C, all adaxial long cells inflated. D, adaxial microhair with basal cell slightly longer than basal cell. A–D, *Ellis 5590*. A, C, $\times 200$; B, $\times 850$; D, $\times 1150$.

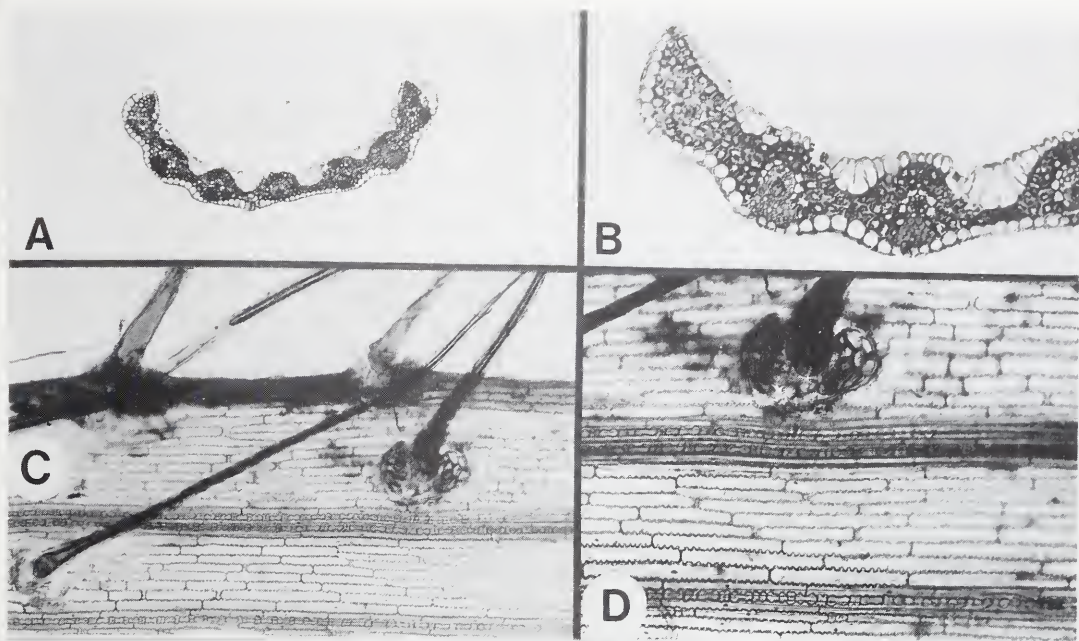


FIGURE 50.1.—*Pentaschistis elegans*: leaf blade anatomy.

A, thin, narrow, slightly inrolled leaf blade.

B, detail of margin showing compact mesophyll, larger abaxial intercostal long cells than the costal ones and alternating first and third order bundles.

C, abaxial epidermis with long, stiff, cushion-based macrohairs.

D, epidermal detail of dumbbell-shaped silica bodies, absence of stomata and large number of modified epidermal cells forming cushion base of macrohair.

A, B, *Ellis* 5982; C, D, *Ellis* 5983. A, $\times 100$; C, $\times 160$; B, D, $\times 250$.

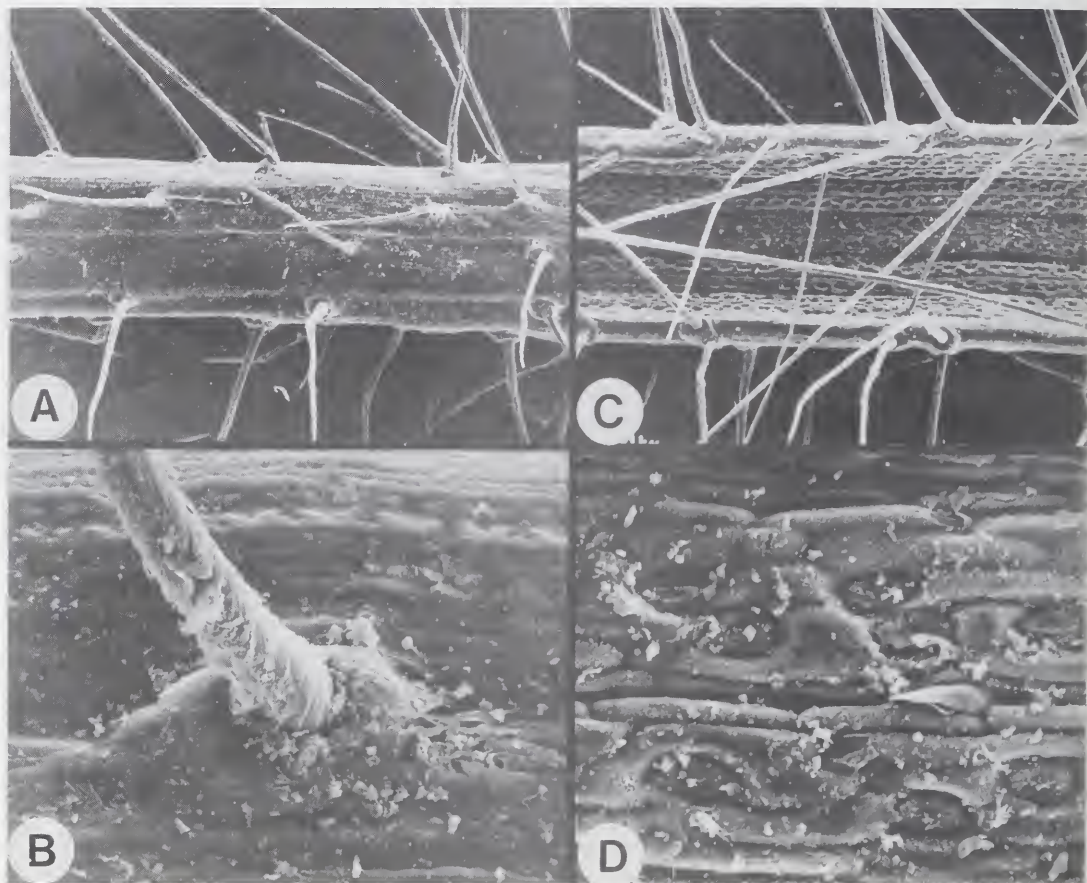
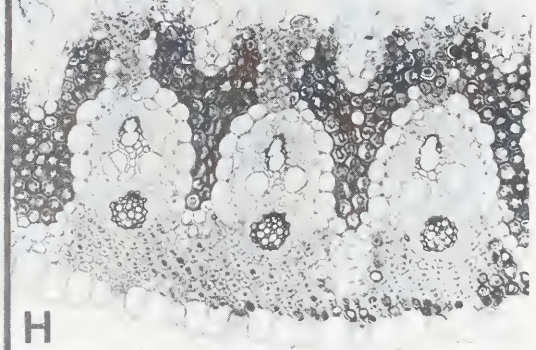
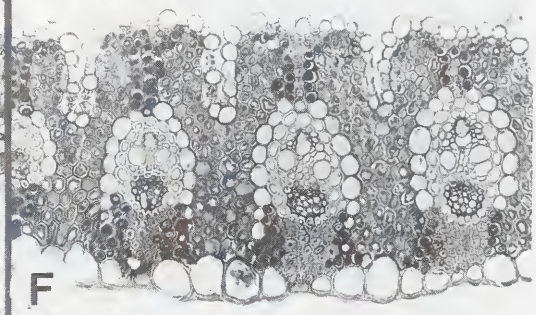
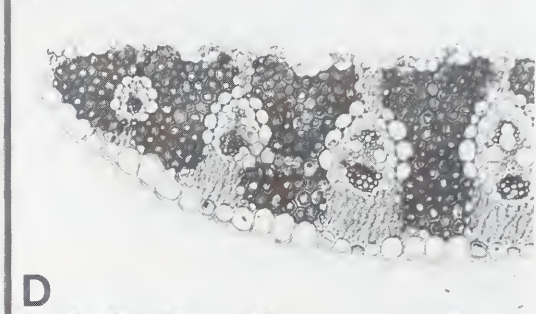
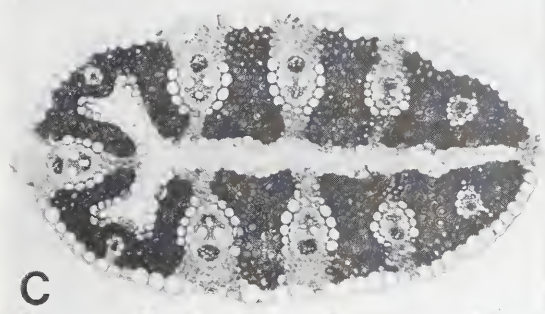
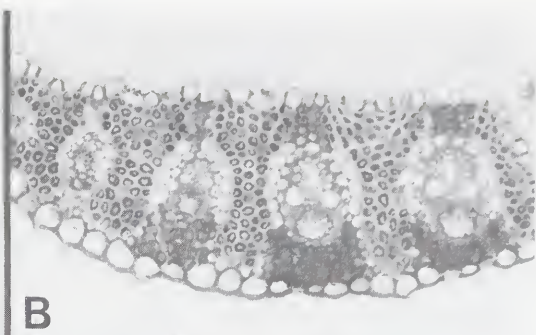
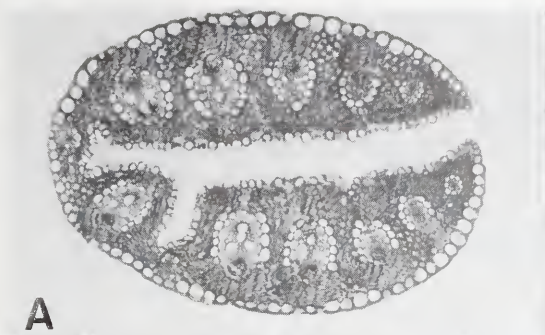


FIGURE 50.2.—*Pentaschistis elegans*: leaf blade ultrastructure. A, B, abaxial epidermis. C, D, adaxial epidermis. A, common and prominent stiff macrohairs on raised bases; no stomata or microhairs observed. B, detail of macrohair base. C, adaxial epidermis with macrohairs very common along lamina margin. D, papillate long cells raised above the level of the stomata. A–D, *Ellis* 5983. A, C, $\times 20$; B, D, $\times 200$.

FIGURE 51.1.—*Pentaschistis tysonii*: leaf blade in tranverse section.

- A, typical leaf outline with deep, cleft-like adaxial furrows only present on either side of the median vascular bundle; note successive first order bundles in each half of lamina.
 - B, detail of compact, isodiametric mesophyll tissue with all chlorenchyma cells with central vacuole; note papillate adaxial epidermal cells and larger abaxial epidermal cells; first order bundles in centre of each half of the lamina adjoin one another.
 - C, typical outline with deep adaxial furrows on either side of median bundle overlying the third order vascular bundles.
 - D, detail of angular chlorenchyma cells compactly arranged; bundle sheath cells conspicuous, without chloroplasts; abaxial sclerenchyma girders well developed.
 - E, typical vascular bundle arrangement with third order bundle adjacent to median bundle but laterally the first order bundles are not separated by smaller bundles; note that deepest adaxial furrow is associated with the third order bundle on either side of the median bundle but that shallower furrows also occur between all the other bundles.
 - F, detail of lateral cleft-like furrows which are shallower than the furrow adjacent to the midrib; note that the fibres of the abaxial girders have both lignified and cellulose secondary walls.
 - G, typical setaceous leaf outline with abaxial epidermal cells much larger than the inflated, papillate adaxial epidermal cells; basic leaf architecture similar to that of all other specimens.
 - H, detail of abaxial and adaxial epidermal cells, chlorenchyma cells, bundle sheath cells and abaxial girders fused laterally.
- A, *Ellis* 3296; B, *Ellis* 3302; C, *Ellis* 3314; D, *Ellis* 3319; E, *Ellis* 3320; F, *Ellis* 3291; G, *Ellis* 3292; H, *Ellis* 1409. G, $\times 160$. A, C, E, $\times 250$; B, D, F, H, $\times 400$.



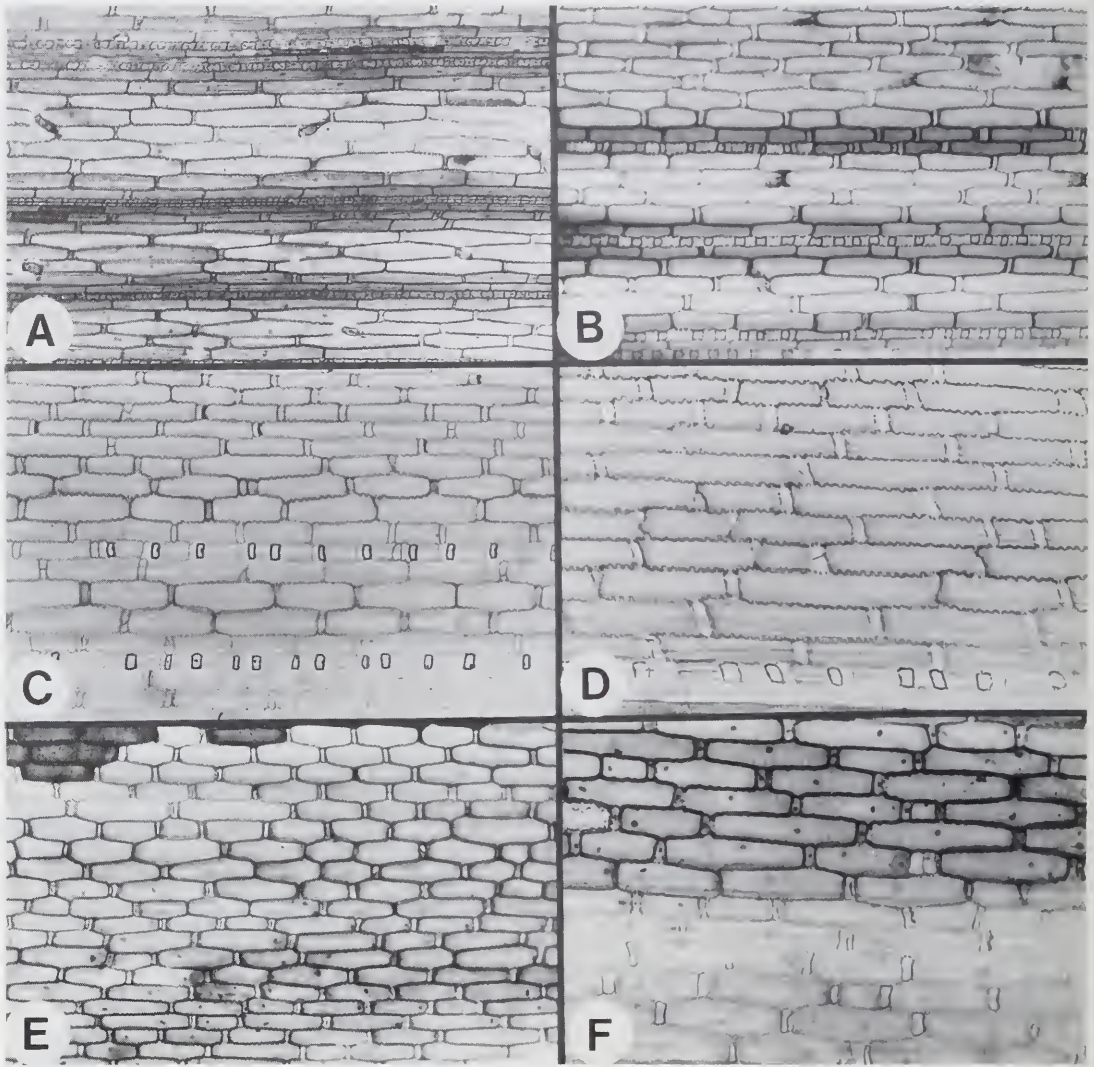


FIGURE 51.2.—*Pentaschistis tysonii*: abaxial epidermal structure.

- A, epidermal cellular pattern showing zonation, absence of stomata, intercostal microhairs and dumbbell-like costal silica bodies.
- B, zonation less distinct with very narrow costal zones with single files of costal cells which are very irregular in shape, the dumbbell shape being almost indistinguishable; note the intercostal long cell separated by tall and narrow cork-silica cell pairs.
- C, specimen in which abaxial epidermal cells are very large; costal and intercostal zones poorly differentiated; costal silica bodies tall and angular.
- D, detail of sinuous walls of intercostal long cells all separated along a file by crenate silica body; costal silica bodies angular to elliptical.
- E, specimen with large abaxial epidermal cells with underlying hypodermal sclerenchyma; note that zonation is not present.
- F, cellular detail of identical intercostal and costal long and short cells; note persistent nuclei.
- A, *Ellis* 5715; B, *Ellis* 3314; C, *Ellis* 3320; D, *Ellis* 3291; E, F, *Ellis* 3292. A–C, E. $\times 250$; D, F, $\times 400$.

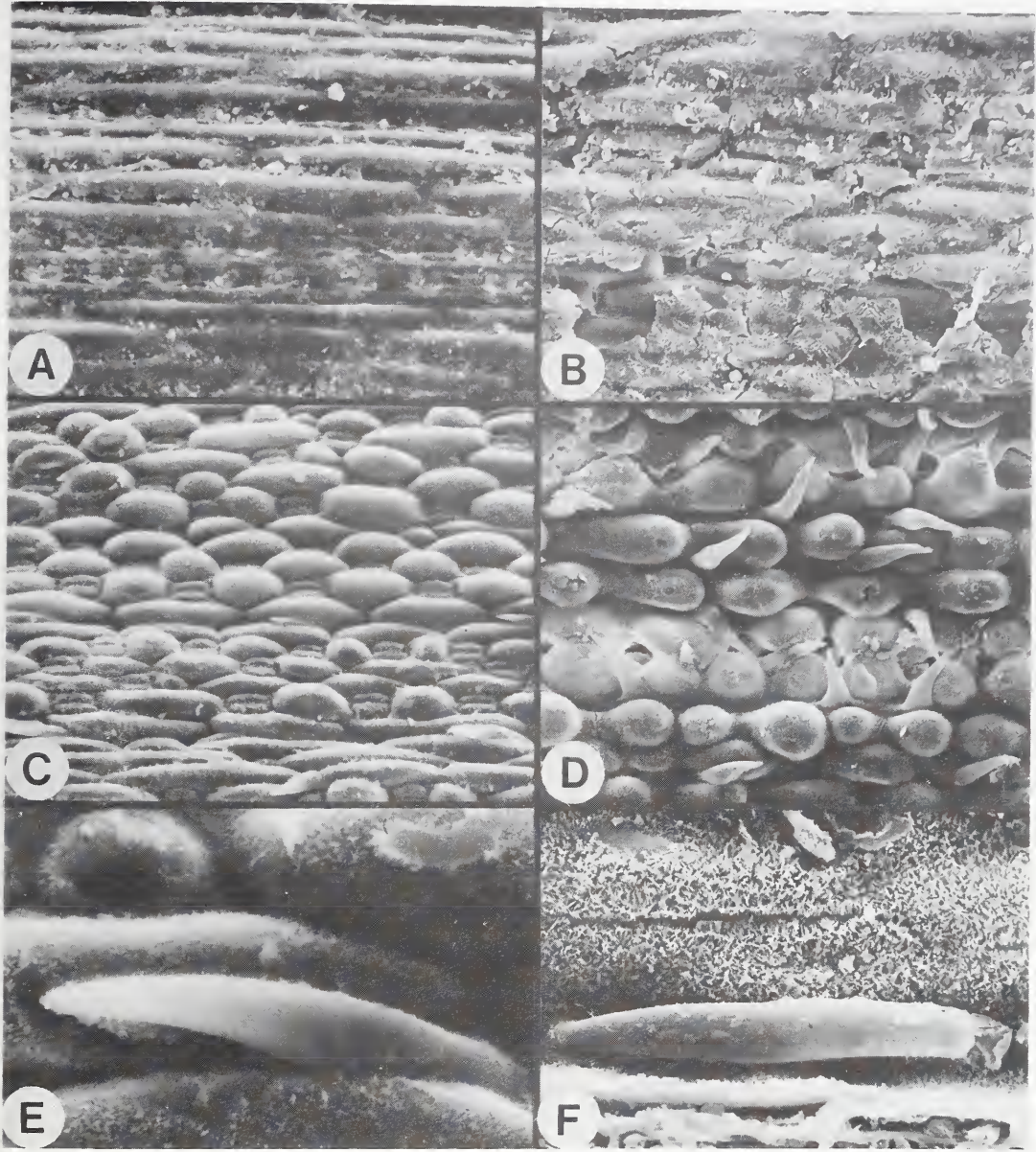


FIGURE 51.3.—*Pentaschistis tysonii*: epidermal ultrastructure. A, B, abaxial epidermis. C–F, adaxial epidermis.

A, narrow, elongated long cells; no appendages.

B, shorter fusiform long cells covered by thick layer of epicuticular wax.

C, papillate adaxial long cells over arching the stomata.

D, very inflated papillae completely over arching the sunken stomata; note costal prickles.

E, adaxial prickly hair and papillate long cells.

F, rare adaxial microhair with very short, collapsed distal cell.

A, C, E, *Ellis* 5715; B, D, F, *Ellis* 3292. A–D, $\times 200$; F, $\times 850$; E, $\times 1000$.

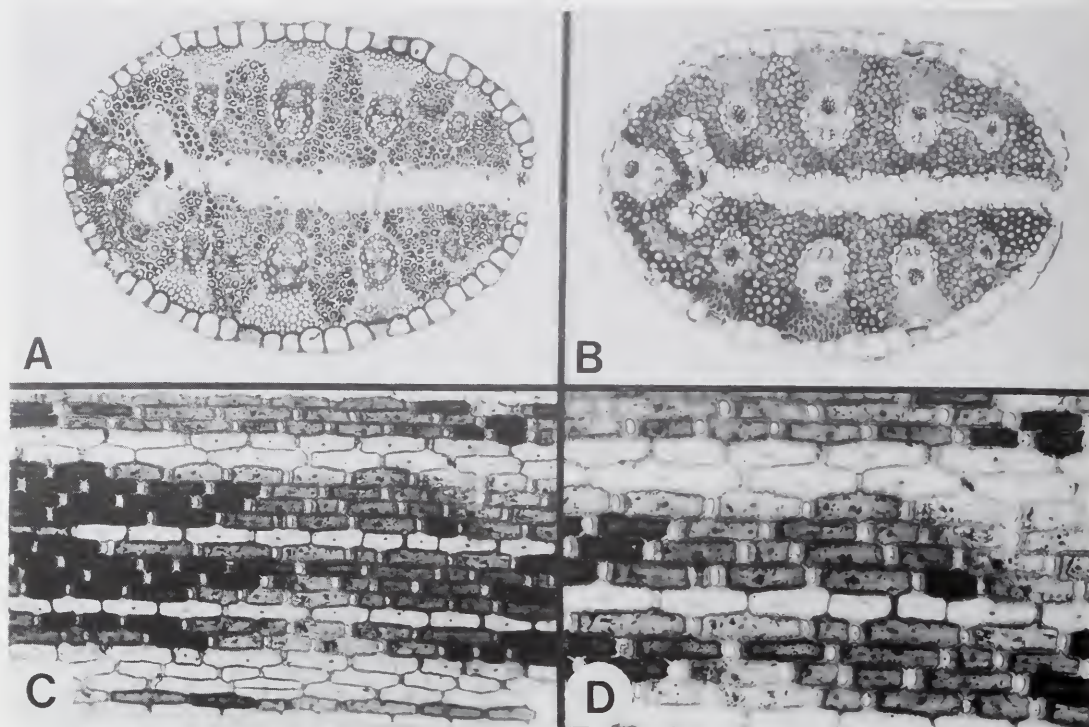


FIGURE 52.1.—*Pentaschistis holciformis*: abaxial epidermis and transectional anatomy.

A, transverse section showing vascular bundle arrangement, deep adaxial furrows on either side of the median vascular bundle only and large abaxial epidermal cells; green filter enhances lignified tissue of abaxial cell walls, mestome sheath and abaxial girders.

B, same section as A with red filter to enhance tissue with cellulose walls—compact chlorenchyma of small, isodiametric cells, colourless outer bundle sheath cells and inflated adaxial epidermal cells.

C, abaxial epidermis with no structural differentiation into costal and intercostal zones although differential staining appears to differentiate between these zones.

D, detail of short, fusiform long cells all separated by cork-silica cell pairs with an elliptical silica body; no stomata or microhairs.

A–D, *Linder* 4866. C, $\times 160$; A, B, D, $\times 250$.

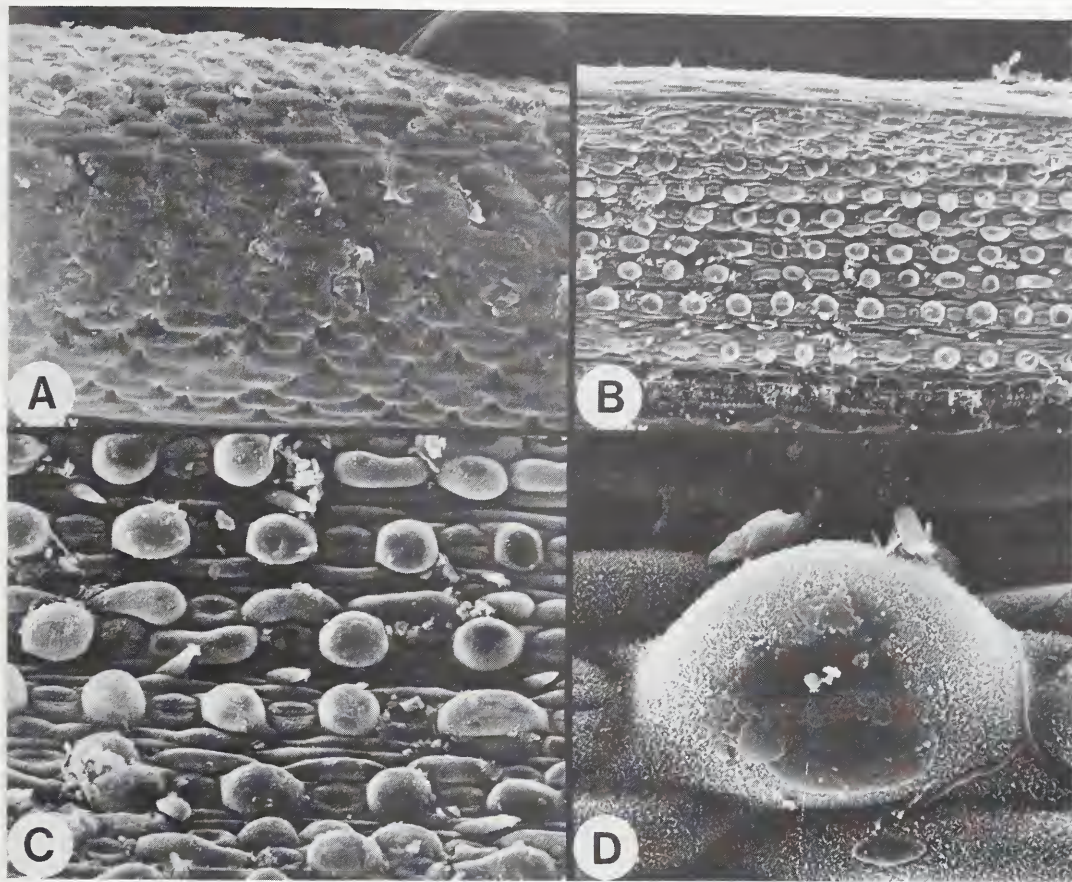


FIGURE 52.2.—*Pentaschistis holciformis*: epidermal ultrastructure.

A, featureless abaxial epidermis with short, slightly inflated long cells.

B, adaxial epidermis with inflated papillae on long cells, particularly the interstomatal cells which overarch the stomata.

C, more detail of the papillate interstomatal cells; note few short prickly hairs.

D, detail of single papillus showing fine epicuticular wax layer and fungal hyphae.

A–D, *Linder* 4866. A, B, $\times 60$; C, $\times 200$; D, $\times 850$.

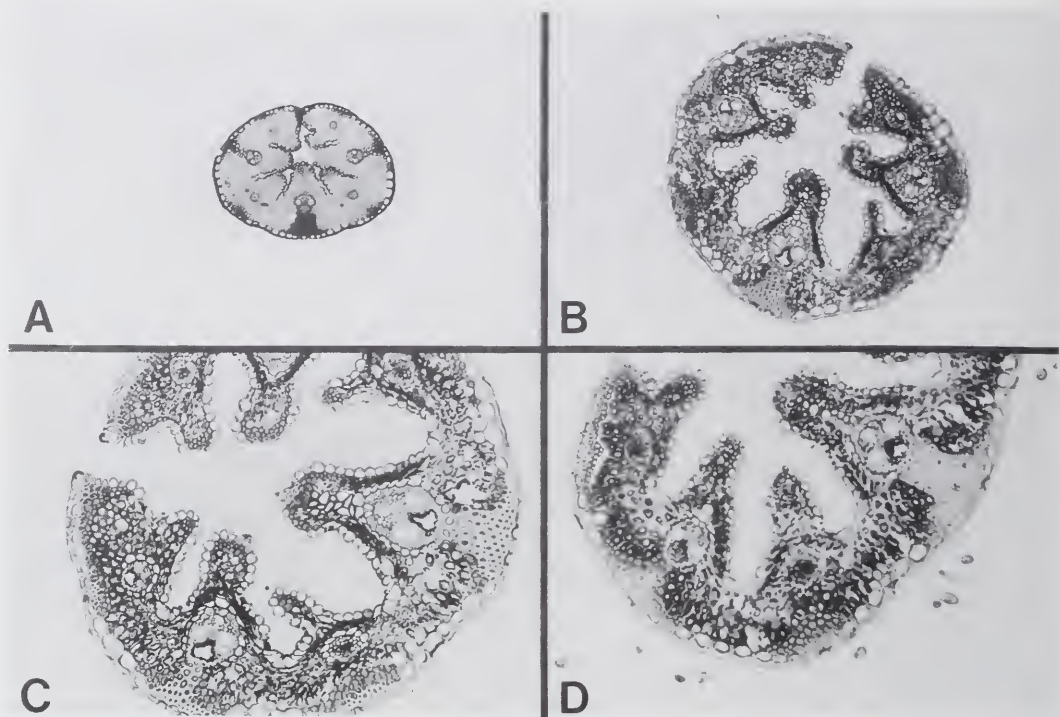


FIGURE 53.1.—*Pentaschistis chippindalliae*: leaf blade in transverse section.

A, tightly setaceous leaf outline with adaxial furrows cleft-like.

B, more open transection with steep-sided furrows; note ribs overlying first order bundles are larger than those associated with smaller bundles.

C, anatomical detail showing bundle sequence and diffuse, poorly preserved mesophyll.

D, adaxial ribs and furrows, diffuse mesophyll.

A, *Ellis 3447*; B, C, *Ellis 4452*; D, *Ellis 3451*. A, $\times 100$; B, $\times 160$; C, D, $\times 250$.

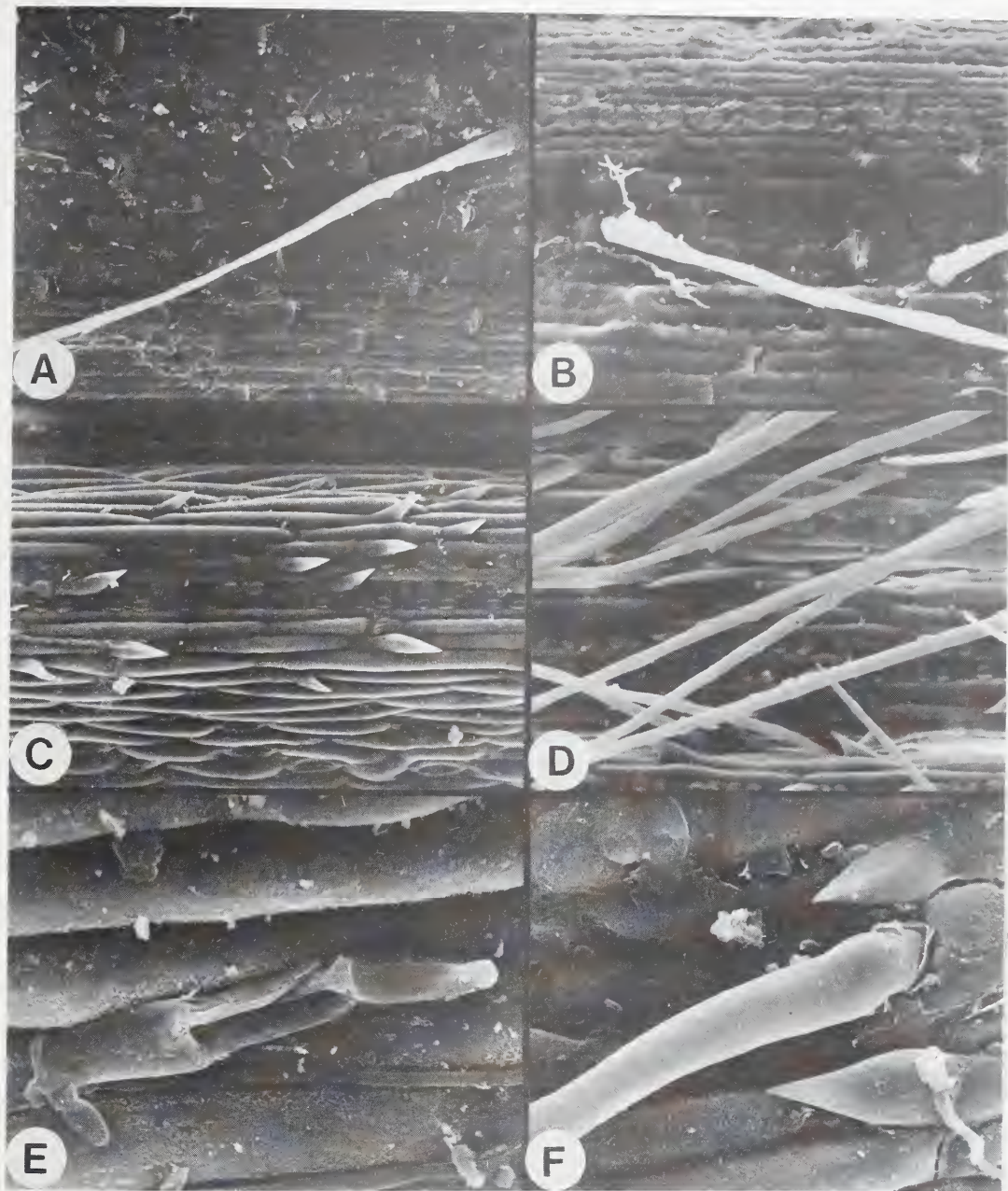


FIGURE 53.2.—*Pentaschistis chippindalliae*: epidermal ultrastructure. A, B, abaxial surface. C–F, adaxial surface. A, featureless epidermis with elliptical silica bodies and stiff macrohair not associated with a raised, cushion base. B, macrohairs and dumbbell-shaped silica bodies. C, adaxial rib with prickles and narrow dumbbell-shaped silica bodies; long cells not papillate. D, pubescent adaxial surface showing long, stiff macrohairs; note dumbbell-shaped silica bodies. E, unusual tricellular microhair. F, base of macrohair not associated with cushion; note short prickles. A, C, E, *Ellis* 5734; B, D, F, *Ellis* 4451. A–D, $\times 200$; F, $\times 700$; E, $\times 1000$.

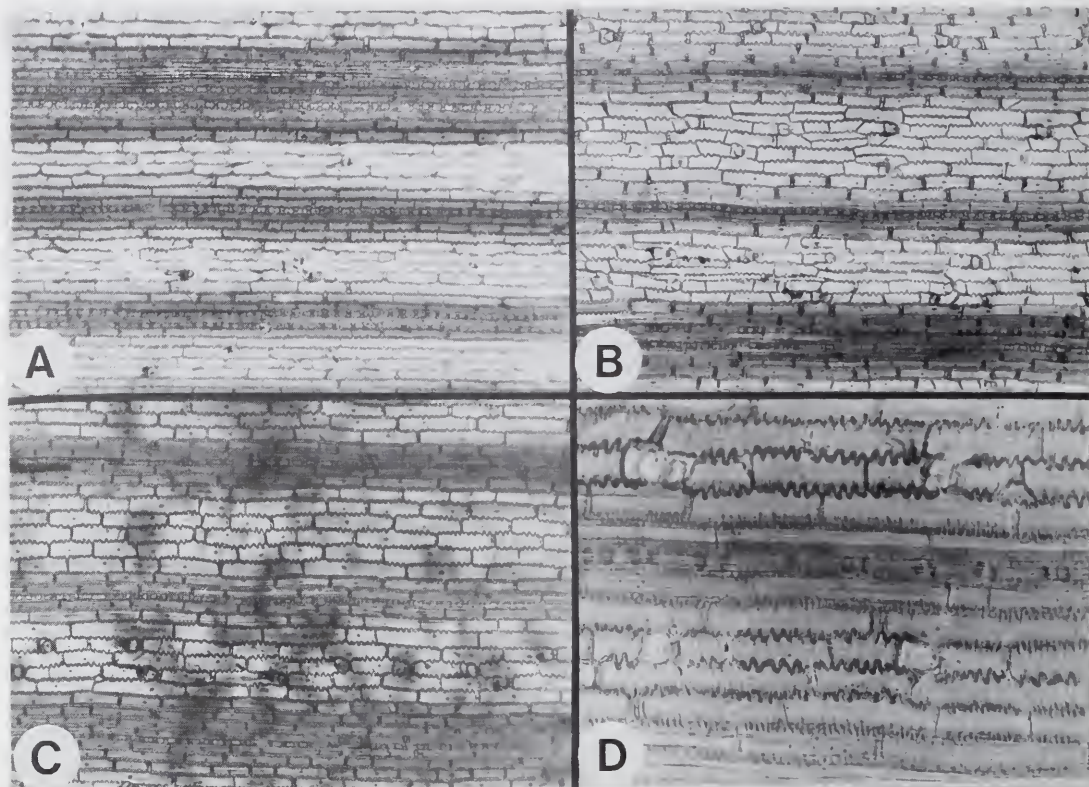


FIGURE 53.3.—*Pentaschistis chippindalliae*: abaxial epidermis.

A, slight zonation evident; note macrohair bases.

B, costal and intercostal zones; macrohair bases associated with irregular intercostal long cells.

C, costal zones identifiable by differential staining but only central file with dumbbell silica bodies; short macrohairs with inflated bases associated with two modified epidermal cells.

D, detail of thick, sinuous anticlinal walls of long cells and pitted periclinal walls; basal cells of macrohairs visible. A, Ellis 4451; B, Ellis 4452; C, Ellis 5734; D, Ellis 3451. A, B, C, $\times 160$; D, $\times 400$.

FIGURE 54.1.—*Pentaschistis exserta*: transectional leaf anatomy.

A, tightly infolded, rounded leaf blade outline.

B, detail of alternating first and third order vascular bundles, continuous abaxial hypodermal layer and abaxial epidermal cells much larger than the adaxial cells; compare the chlorenchyma tissue of compact, isodiametric cells which differs somewhat from the more diffuse chlorenchyma tissue of less angular cells of Figures H, I.

C, interference contrast illumination showing narrow adaxial channel with an adaxial furrow present on either side of the median vascular bundle only.

D, detail of sclerenchyma tissue with thin, but continuous, hypodermal layer; note smaller vascular bundles without associated abaxial girders; chlorenchyma tissue more diffuse than in B, with air spaces visible.

E, typical outline with adaxial furrows on either side of median vascular bundle only; mesophyll tissue rather compact.

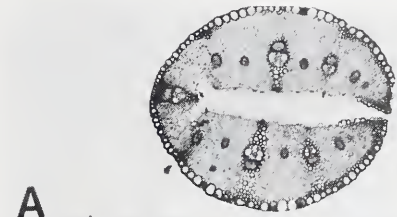
F, sclerenchyma tissue with either cellulose (darkly stained) or lignified secondary walls.

G, alternating larger and smaller vascular bundles; note relative size of abaxial and adaxial epidermal cells.

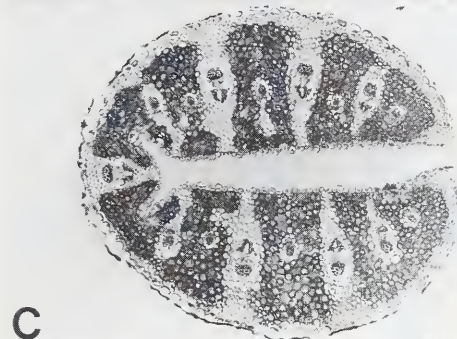
H, detail of alternating first and third order vascular bundles, somewhat diffuse mesophyll tissue and two different cell types in abaxial sclerenchyma girders.

I, detail of typical anatomy.

A, B, Ellis 5688; C, D, Du Toit 646; E, Ellis 5724; F, Ellis 5723; G, Ellis 5696; H, Ellis 3169; I, Du Toit 2301. A, $\times 100$; C, $\times 160$; B, D–G, $\times 250$; H, I, $\times 400$.



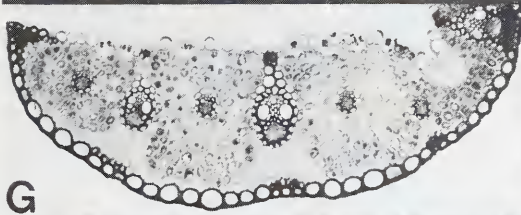
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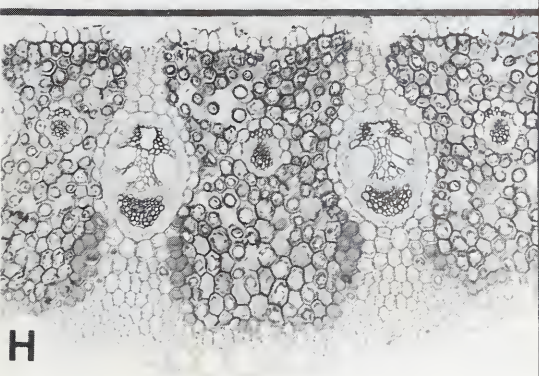
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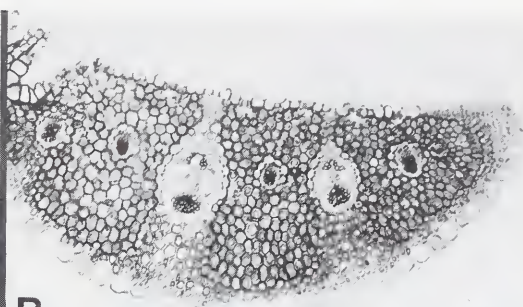
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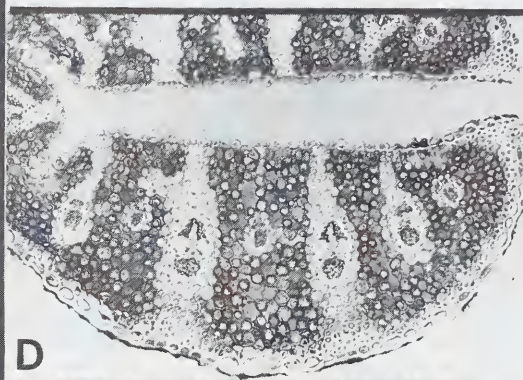
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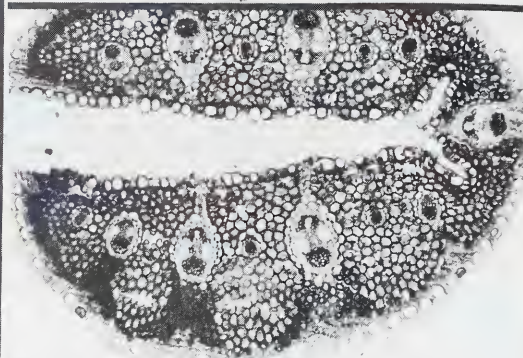
H



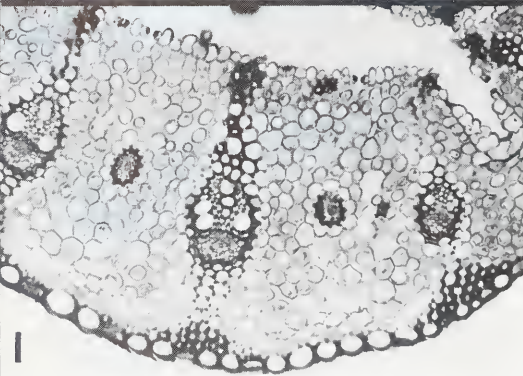
B



D



F



I

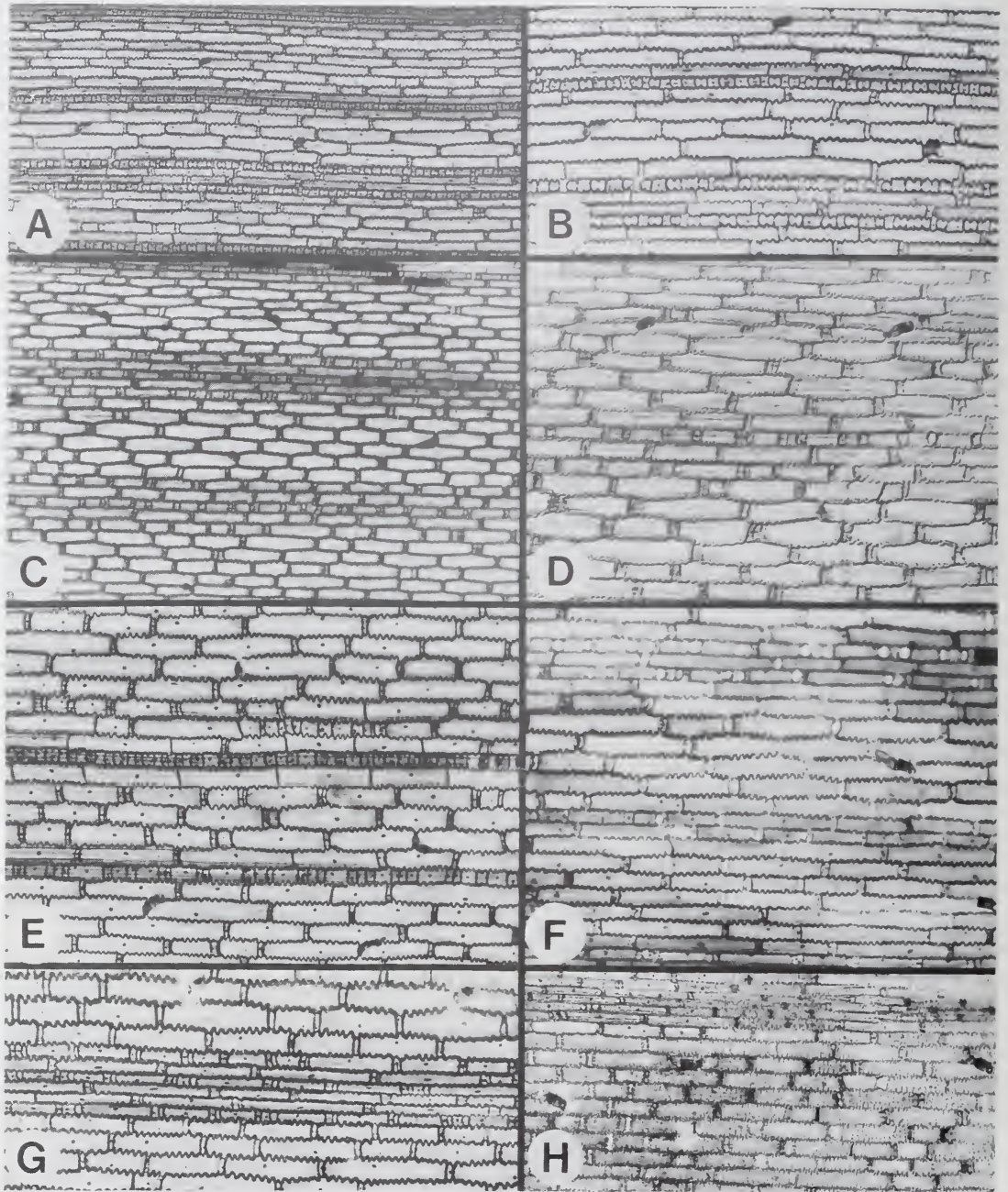


FIGURE 54.2.—*Pentaschistis exserta*: abaxial epidermal structure.

A, zonation evident but no abaxial stomata.

B, dumbbell-shaped costal silica bodies, rectangular intercostal long cells alternate with tall and narrow silica bodies; note intercostal microhairs.

C, epidermal zonation distinguishable although the costal and intercostal cells are not highly differentiated.

D, costal silica bodies very variable, with very few being dumbbell-shaped; intercostal long cells fusiform; microhairs with distal cell longer than basal cell.

E, costal zones with irregular dumbbell-shaped silica bodies; nucleate, rectangular long cells.

F, silica bodies elliptical and long cells slightly fusiform; microhairs with longer distal cell.

G, slightly fusiform long cells with thick, sinuous walls; silica body shape very variable.

H, epidermal cells with very thick, pitted walls; note microhairs.

A, B, *Ellis* 5724; C, D, *Ellis* 5688; E, *Ellis* 5713; F, *Ellis* 5700; G, *Ellis* 5696; H, *Ellis* 5723. A, C, $\times 160$; B, D–H, $\times 250$.

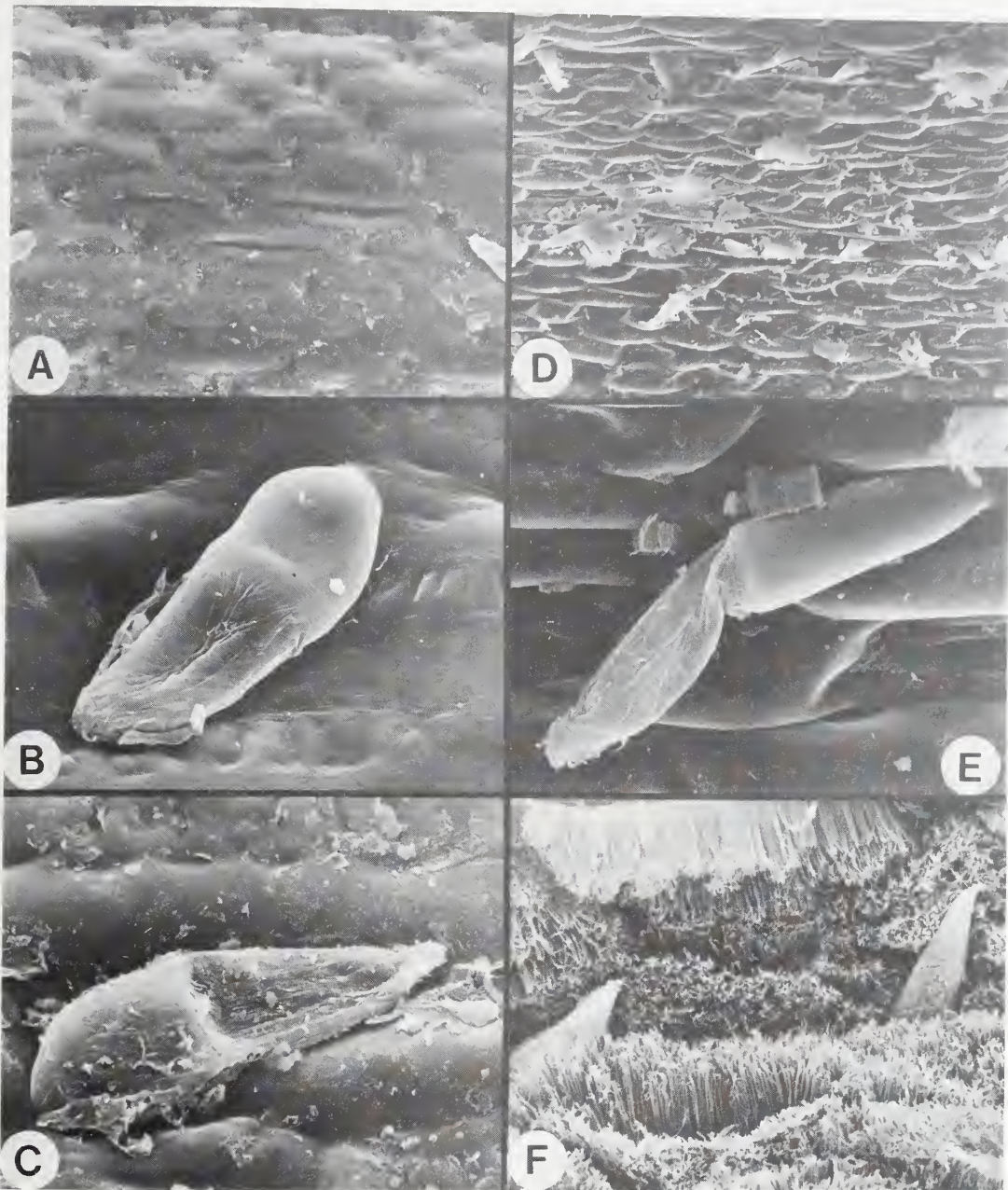


FIGURE 54.3.—*Pentaschistis exserta*: SEM of epidermal surfaces. A–C, abaxial epidermis. D–F, adaxial epidermis. A, intercostal zone with short long cells with thickened, sinuous anticlinal walls. B, abaxial microhair with distal cell longer than basal cell. C, abaxial microhair also with the tapering distal cell longer than the basal cell. D, adaxial surface with long cells with inflated periclinal walls but these not papillate. E, adaxial microhair thinner than those on the abaxial surface and with the two cells of equal length. F, adaxial surface with very well-developed epicuticular rods. A, B, D, E, *Ellis 5687*; C, *Ellis 5724*; F, *Ellis 5700*. A, D, $\times 200$; F, $\times 650$; C, $\times 970$; B, $\times 1000$; E, $\times 1300$.

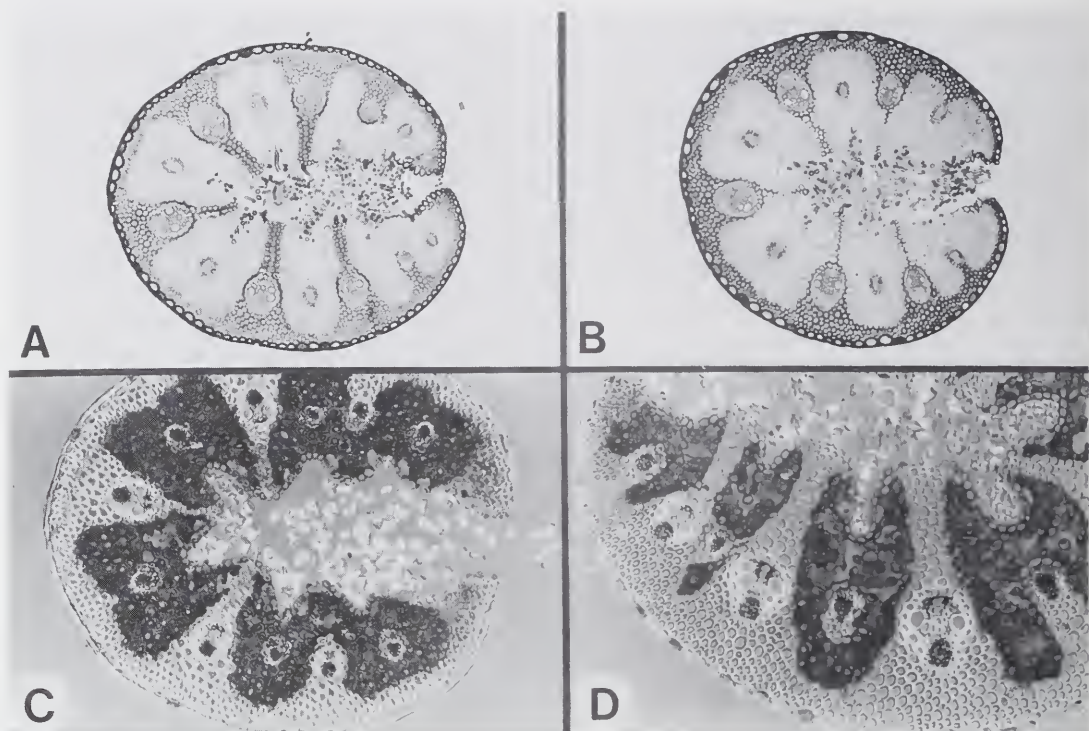


FIGURE 55.1.—*Pentaschistis basutorum*: leaf blade in transverse section.

A, rounded, tightly infolded leaf outline; note alternating first and third order vascular bundles.

B, typical leaf outline and vascular bundle arrangement; note sectioned hairs in adaxial channel.

C, interference contrast showing refracting lignified tissue—sclerenchyma fibres and adaxial macrohairs; continuous hypodermal layer present and third order bundles not associated with girders.

D, interference contrast showing thin-walled fibres of girders associated with first order bundles and of the hypodermal layer; note diffuse nature of the mesophyll tissue with large air spaces visible.

A, Ellis 2368; B, Ellis 2373; C, Ellis 2369; D, Ellis 2370. A, B, $\times 160$; C, D, $\times 250$.

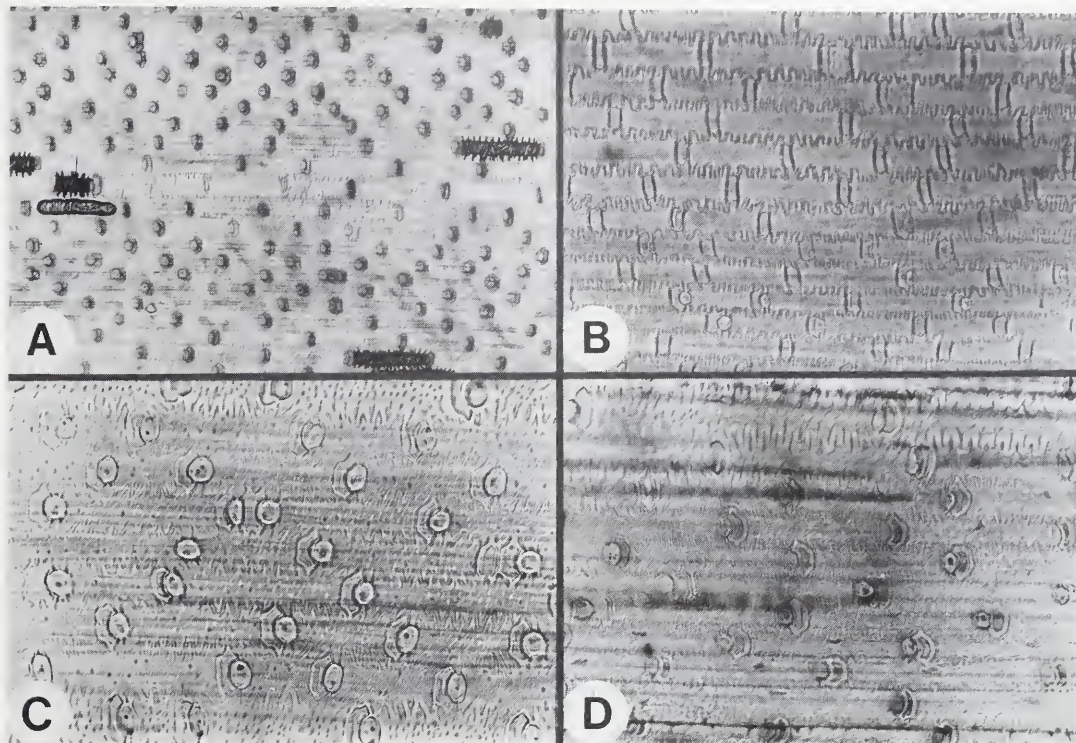


FIGURE 55.2.—*Pentaschistis basutorum*: abaxial epidermis.

- A, epidermal zonation not evident with costal and intercostal zones not distinguishable; no stomata or microhairs present.
 B, detail of long cells with very sinuous and pitted walls alternating with cork-silica cell pairs; silica bodies small, elliptical and enfolded in crescentic cork cell; no microhairs.
 C, detail of cork-silica cell pairs and pitted long cell periclinal walls.
 D, detail of crescentic cork cells enfolding elliptical silica bodies; note very thick, sinuous anticlinal long cell walls.
 A, Liebenberg 7454; B, Ellis 2367; C, Ellis 2369; D, Ellis 2368. A, $\times 250$; B, $\times 400$; C, D, $\times 640$.

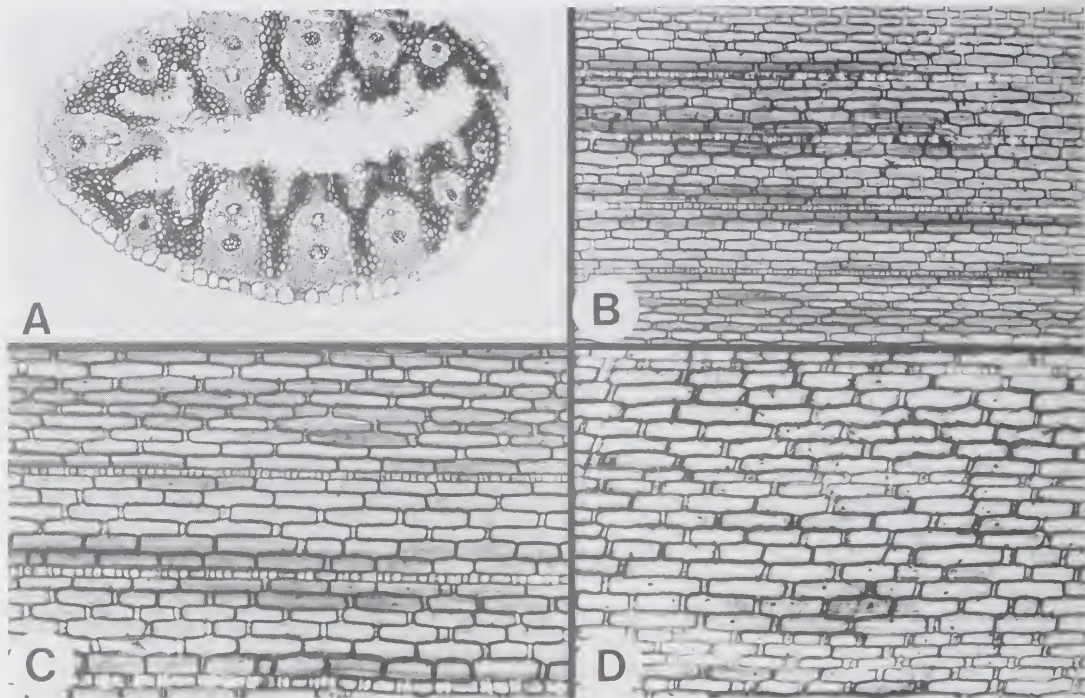


FIGURE 56.1.—*Pentaschistis praecox*: leaf blade anatomy.

- A, transectional anatomy showing deepest adaxial furrows situated on either side of the median vascular bundle with the other furrows being shallower; laterally several first order vascular bundles adjoin one another; the abaxial epidermal cells are considerably larger than the inflated adaxial epidermal cells.
 B, indistinct abaxial epidermal zonation although costal zones are discernible.
 C, detail of very irregularly dumbbell-shaped costal silica bodies, shortly fusiform intercostal long cells separated along files by cork-silica cell pairs with both cells tall and narrow; no stomata or appendages visible.
 D, epidermis in which zonation not evident; no dumbbell-shaped silica bodies.
 A–C, Wright 461; D, Manning, Hilliard & Burt 15939. B, $\times 160$; A, C, D, $\times 250$.

FIGURE 57.1.—*Pentaschistis curvifolia*: characteristic transectional leaf anatomy.

- A, slightly inrolled but, nevertheless, expanded outline; note relative thickness of margin in comparison to the centre of the lamina.
 B, expanded blade type with noticeably thickened margins.
 C, wide, expanded blade becoming gradually thicker towards the margin; first and third order vascular bundles alternate across the leaf width.
 D, expanded blade with thickened margin in which the bundle sequence and adaxial rib structure is modified.
 E, typical anatomy of the midlamina with alternating large and small bundles, flat-topped adaxial ribs overlying the larger bundles, sclerophyllous mesophyll and abaxial epidermal cells uniformly larger than the adaxial epidermal cells.
 F, detail of thickened margin with fused abaxial girders associated with the lateral first order bundles which are located beneath massive ribs; the third order bundles do not have associated ribs as occurs in the midlamina; note very large abaxial epidermal cells and compact mesophyll.
 G, marginal detail with massive trapezoidal, fused abaxial girders associated with the first order vascular bundles.
 H, detail of margin with narrow, cleft-like adaxial furrows with U-shaped chlorenchyma tissue in which is located a third order bundle under the furrow; note the extremely thick secondary walls of the sclerenchyma fibres and the abaxial silica cells in section.
 A, Ellis 2216; B, Ellis 2225; C, Ellis 5485; D, G, Ellis 2518; E, Ellis 2301; F, Ellis 2224; H, Ellis 2492. A–D, $\times 100$; E–H, $\times 250$.



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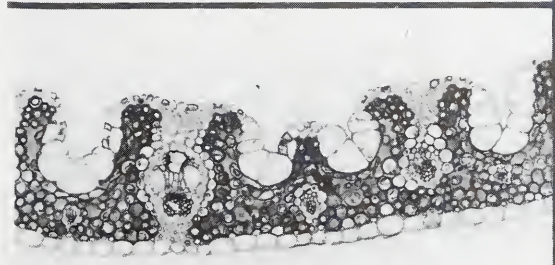
B



C



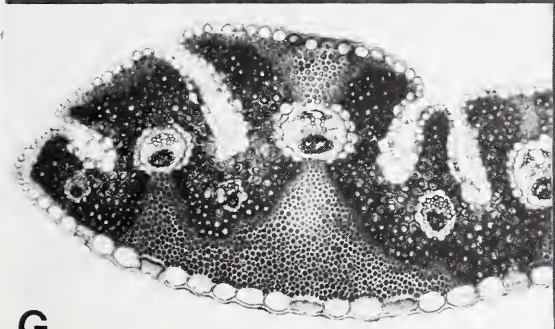
D



E



F



G



H

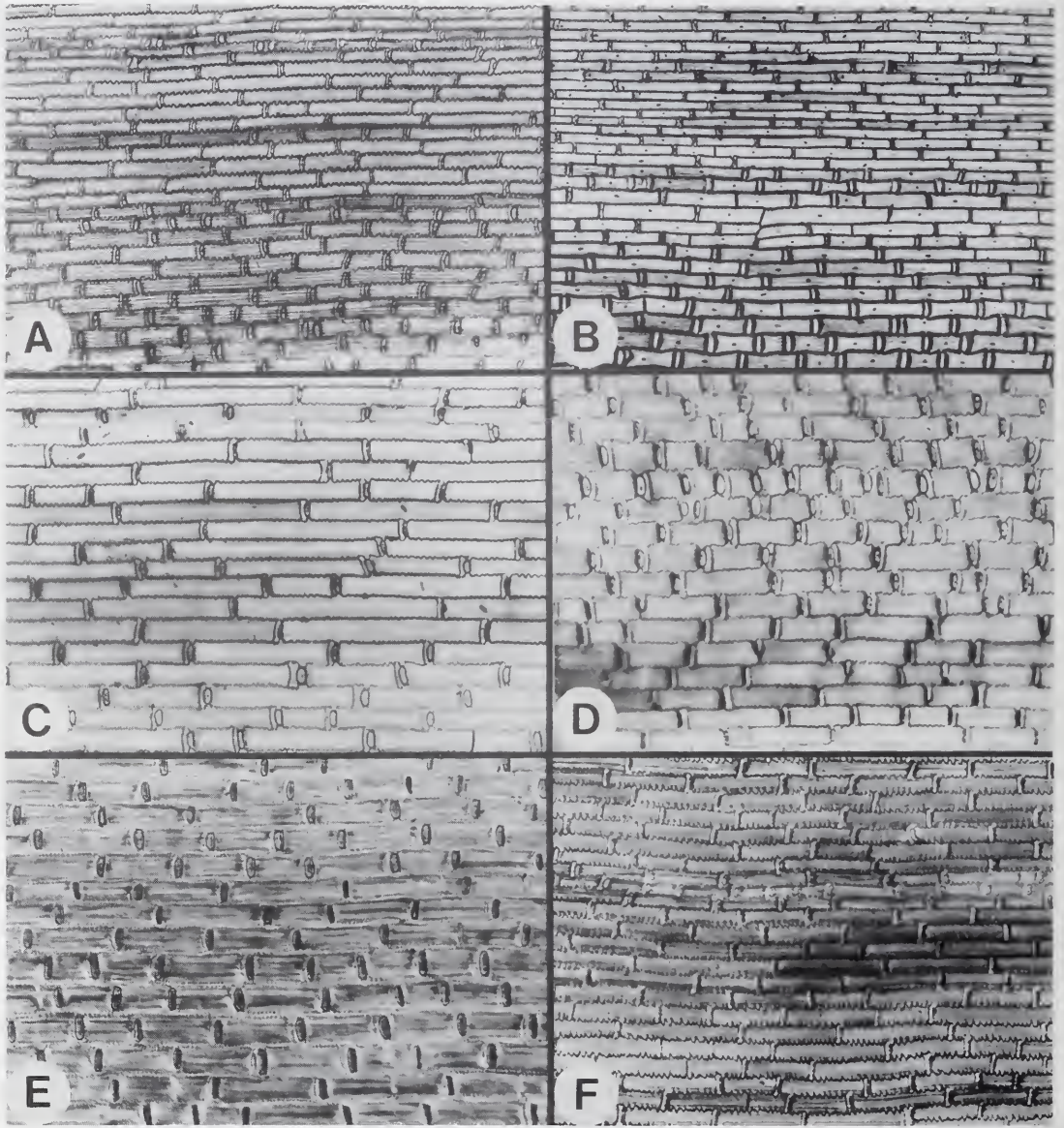


FIGURE 57.2.—*Pentaschistis curvifolia*: abaxial epidermal structure.

A, zonation not evident; note gradual increase in cell size as larger cells overlying the thickened margin are approached (from top to bottom in figure).

B, width of cell files increasing over thick margin; all long cells separated by cork-silica cell pairs; no stomata or microhairs.

C, typical cell configuration with rectangular long cells separated by pairs of short cells with the silica body tall, elliptical.

D, detail of silica and cork cells.

E, interference contrast showing tall, elliptical silica bodies located between all long cells which are arranged in a brickwork pattern.

F, tall and narrow silica bodies and sinuous long cell walls.

A, *Ellis* 2513; B, *Ellis* 5485; C, *Ellis* 2322; D, *Ellis* 625; E, *Ellis* 2351; F, *Ellis* 2354. A, B, $\times 160$; C–F, $\times 250$.

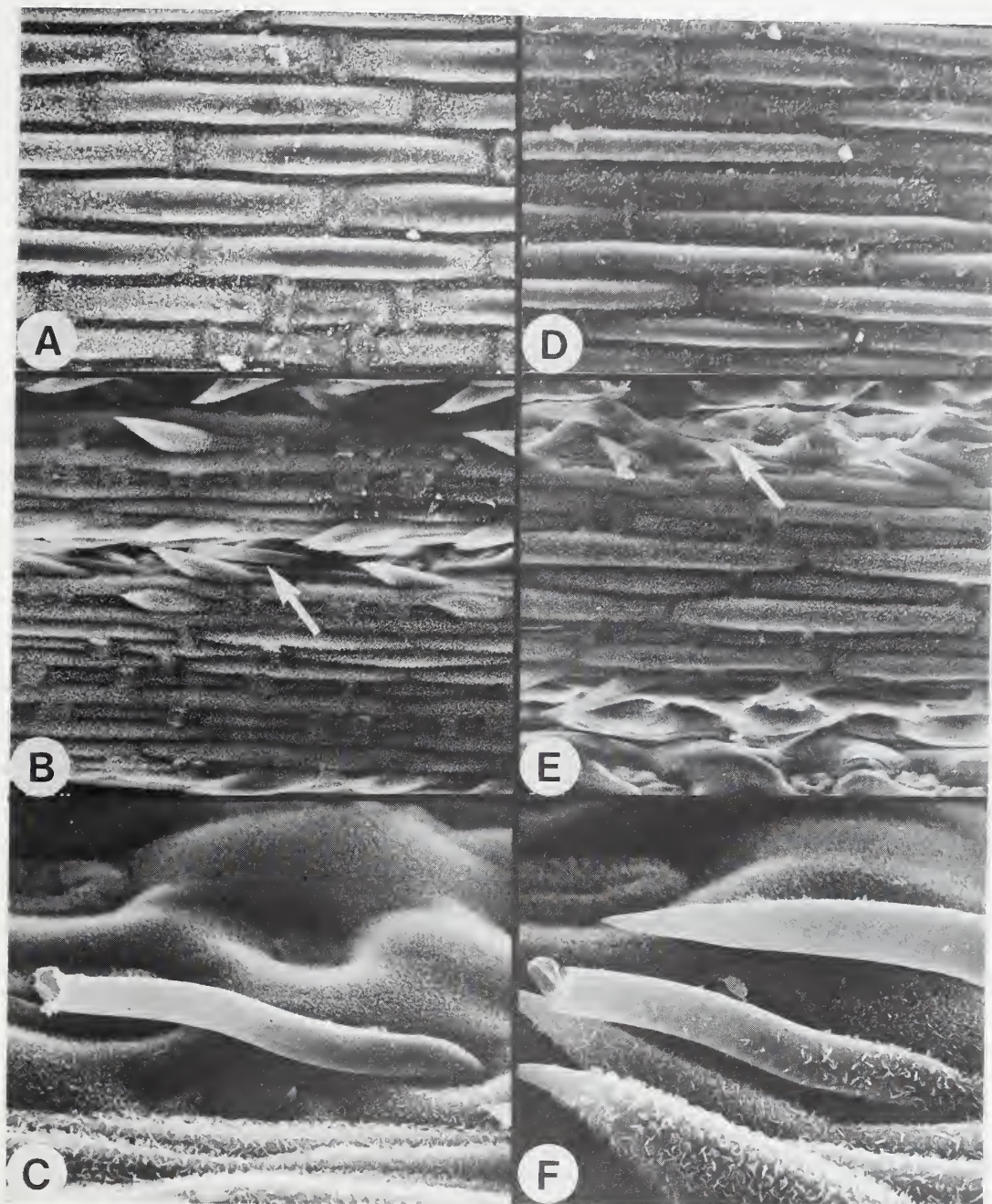


FIGURE 57.3.—*Pentaschistis curvifolia*: epidermal ultrastructure. A, D, abaxial epidermis; B, C, E, F, adaxial epidermis.

A, typical brickwork arrangement of elongated, rectangular long cells; long cells alternate with cork-silica cell pairs. B, adaxial epidermal surface with interlocking costal prickles overlying cleft-like furrows; note microhairs in furrows (arrowed).

C, elongate adaxial microhair with minute, deciduous distal cell.

D, elongated, rectangular abaxial long cells.

E, adaxial surface with costal long cells and prickles on the sides of the adaxial ribs; these prickles overlie the furrows in which the microhairs occur (arrowed).

F, adaxial microhair and prickles.

A–C, *Ellis 5485*; D–F, *Ellis 5610*. A, B, D, E, $\times 200$; C, $\times 700$; F, $\times 900$.

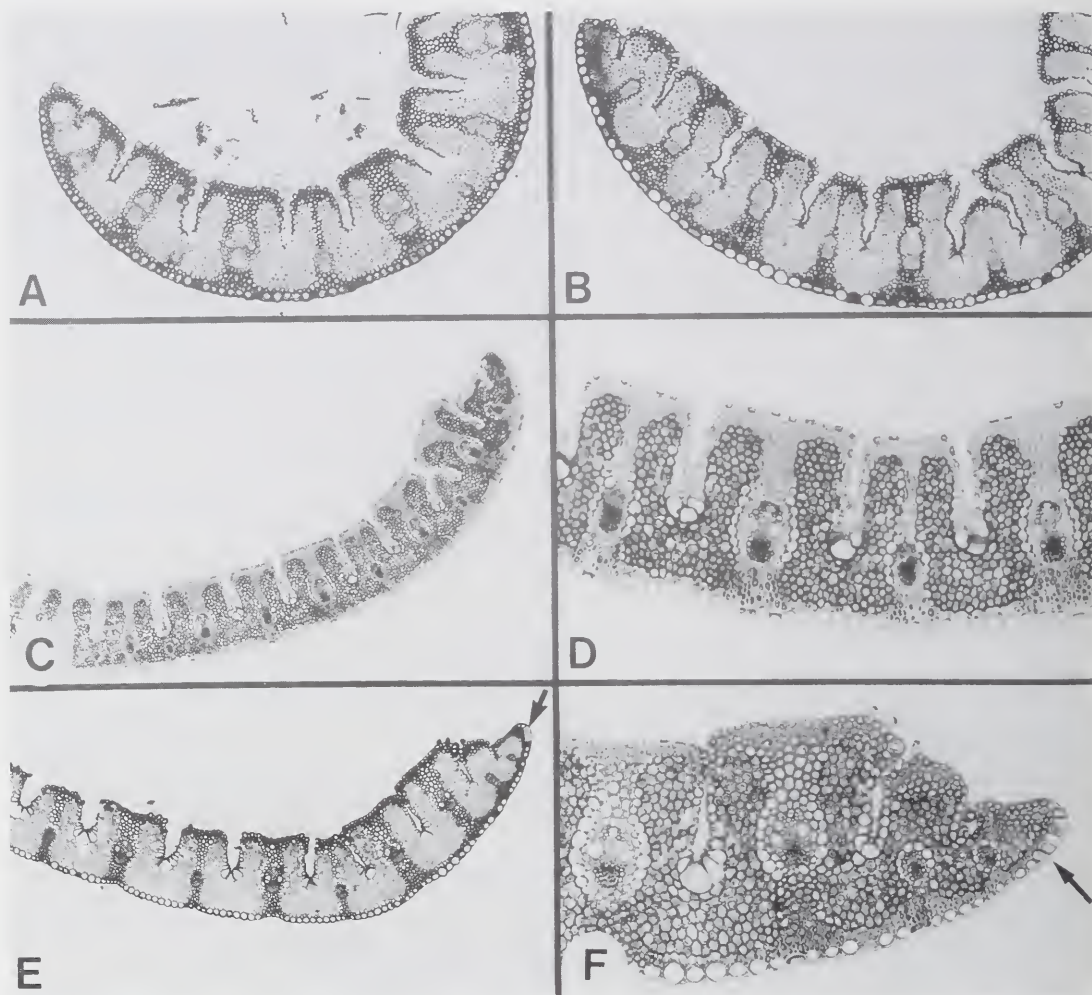


FIGURE 58.1.—*Pentaschistis pungens*: leaf transverse sections.

A, inrolled outline of specimen with slightly tapering margins; margins not thickened; note hypodermal sclerenchyma layer and thickened abaxial epidermal cells.

B, inrolled outline but margin abrupt and lateral part of lamina slightly thicker than central part; alternating sequence of first and third order bundles.

C, expanded outline showing enlarged lateral adaxial ribs; note flat-topped adaxial ribs and cleft-like furrows associated with all vascular bundles.

D, detail of well-developed, anchor-shaped, lignified adaxial girders, cleft-like furrows with bulliform cells at their bases, a thin abaxial hypodermal layer of fibres and typical sclerophyllous type mesophyll tissue.

E, lateral thickening of lamina and sessile linear gland (arrowed) on narrow projection in extreme margin.

F, detail of modified anatomy associated with thickened margin; note massive penultimate rib and sclerenchyma arrangement; sessile linear gland cells visible in marginal projection (arrowed).

A, *Ellis* 2506; B, *Ellis* 2488; C, D, *Ellis* 5795; E, F, *Ellis* 5516. C, E, $\times 100$; A, B, $\times 160$; D, F, $\times 250$.

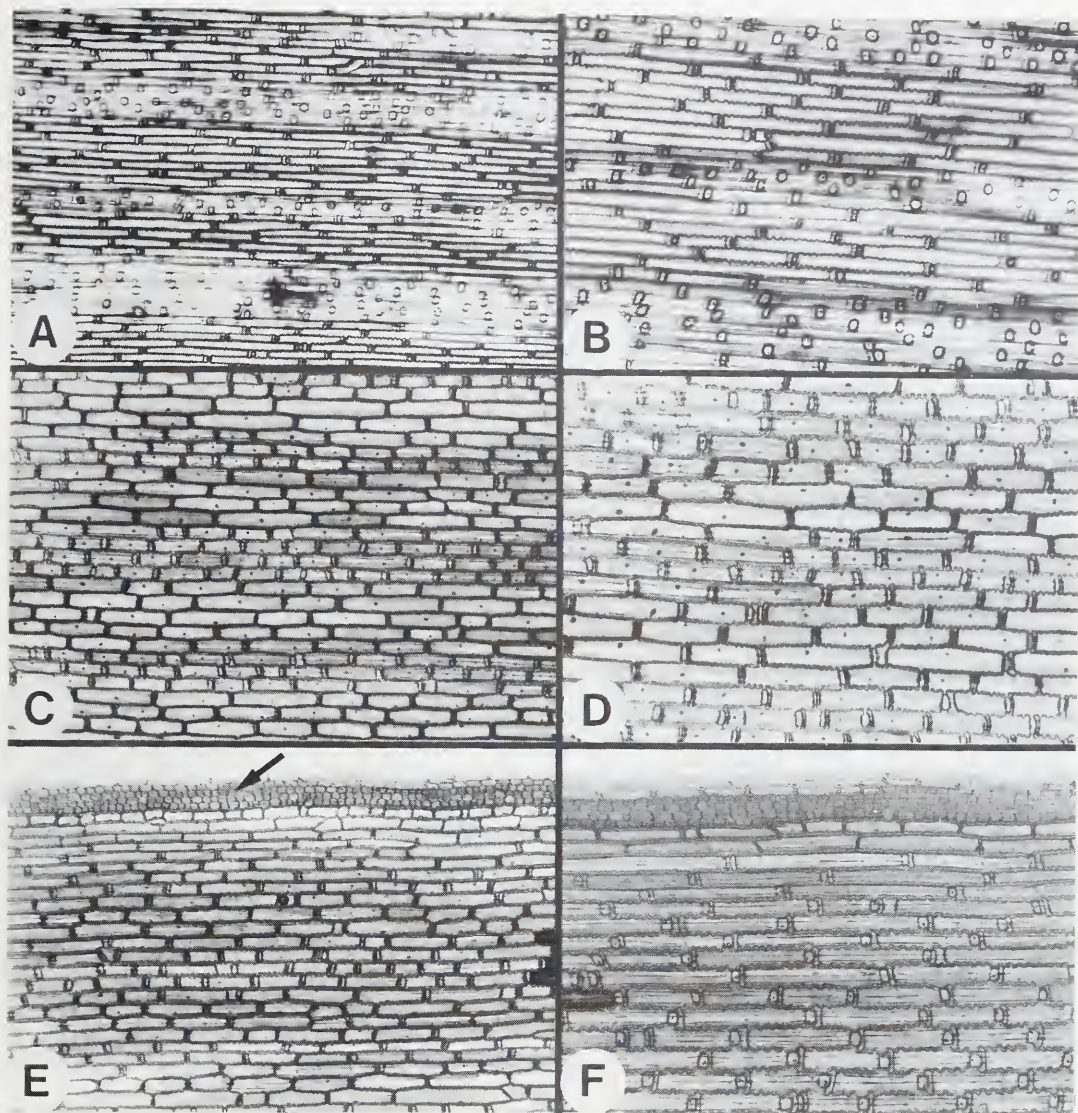


FIGURE 58.2.—*Pentaschistis pungens*: abaxial epidermal structure.

A, slight degree of epidermal zonation evident with costal and intercostal zones distinguishable.

B, detail of epidermal cells with silica bodies and long cells of costal and intercostal zones differing in structure and shape; no stomata or microhairs.

C, typical epidermal pattern in which zonation is hardly distinguishable; long cell size consistent throughout epidermis and only costal silica bodies slightly more elliptical than those of intercostal zones.

D, detail showing similar cell structure throughout epidermis; costal and intercostal long cells identical in shape and only costal silica bodies slightly more developed.

E, lateral part of blade showing continuous linear gland along margin (arrowed).

F, detail of small marginal linear glandular cells and uniform pattern of arrangement of epidermal cells.

A, B, *Ellis* 2488; C, D, *Ellis* 579f; E, *Ellis* 5516; F, *Ellis* 558l. A, C, E, $\times 160$; B, D, F, $\times 250$.

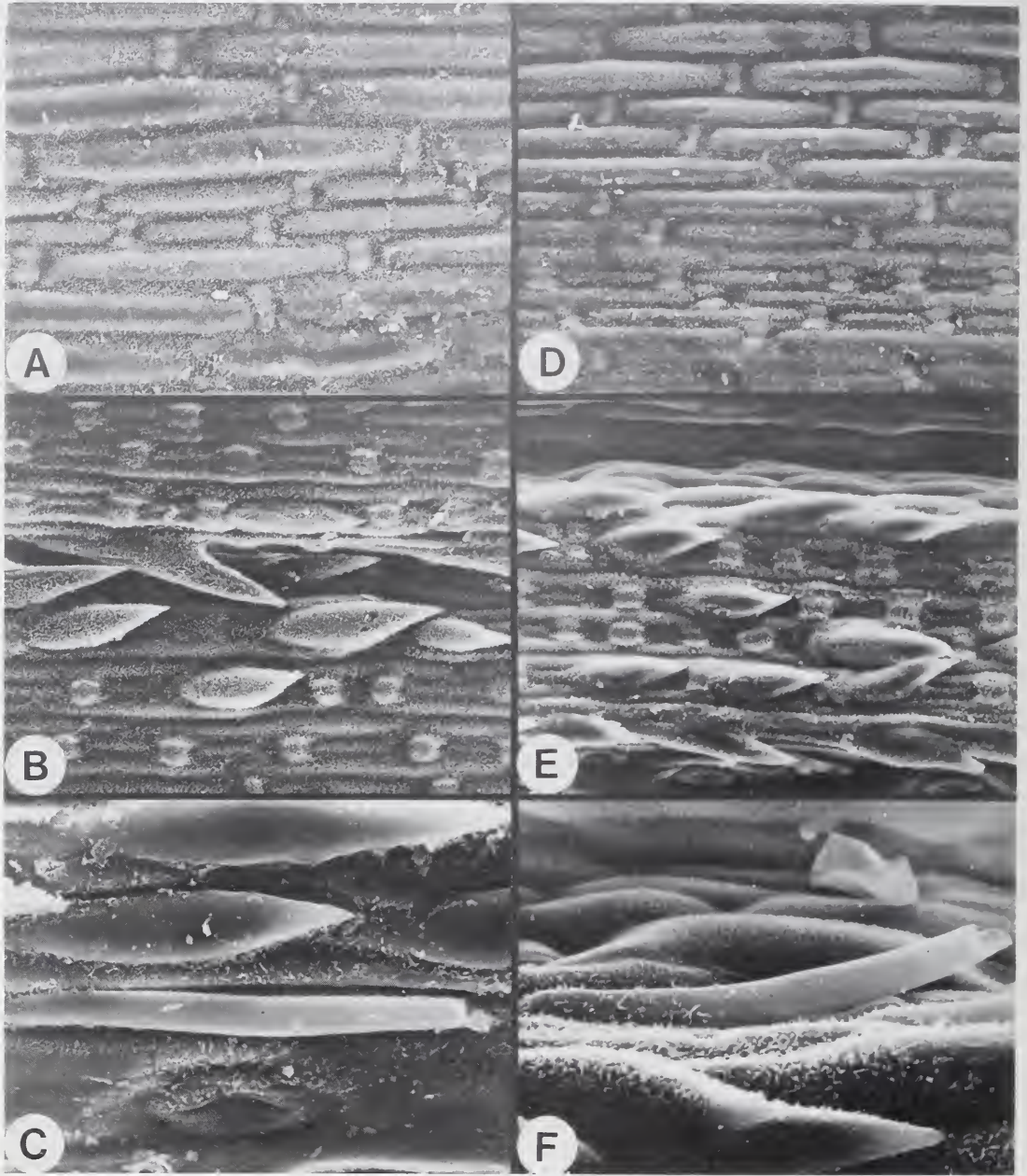


FIGURE 58.3.—*Pentaschistis pungens*: epidermal ultrastructure. A, D, abaxial epidermis. B, C, E, F, adaxial epidermis.

A, brickwork pattern of long cell arrangement; note long cells alternate with silico-suberose couples.

B, adaxial rib with interlocking prickles overlying furrow.

C, finger-like adaxial microhair with minute, deciduous distal cell.

D, abaxial epidermal pattern.

E, adaxial rib with saddle-shaped silica bodies and prickle hairs.

F, typical microhair with very small distal cell.

A–C, *Ellis 5516*; D–F, *Ellis 5581*. A, B, D, E, $\times 200$; C, $\times 550$; F, $\times 650$.

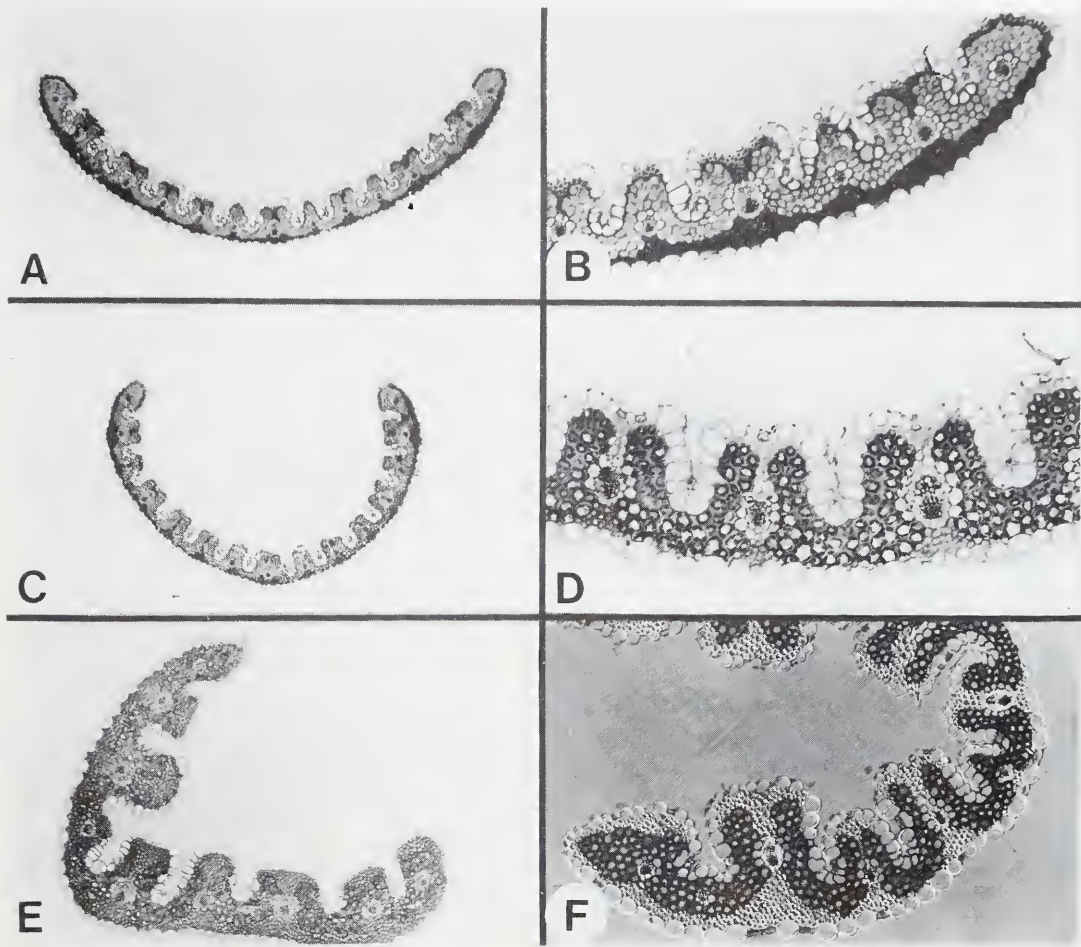


FIGURE 59.1.—*Pentaschistis acinosa*: leaf blade in transverse section.

A, leaf outline showing slight thickening of lamina laterally.

B, abrupt margin with conspicuous abaxial hypodermal sclerenchyma layer; note bulliform-like adaxial epidermal cells on the sides of the furrows; these cells similar in cross sectional area to the abaxial epidermal cells.

C, slightly incurved blade outline.

D, anatomical detail of compact mesophyll and conspicuous epidermal cells with thick peripheral walls; note large, inflated bulliform-like adaxial epidermal cells, particularly those located on the sides and bases of furrows.

E, outline of narrower, more infolded leaf blade with very well-developed hypodermal tissue.

F, interference contrast showing refracting sclerenchyma and epidermal cells; note anchor-shaped adaxial girders..

A, B, *Ellis 5560*; C, *Ellis 5550*; D, *Ellis 2267*; E, *Ellis 2278*; F, *Ellis 2340*. A, C, E, $\times 100$; B, F, $\times 250$; D, $\times 400$.

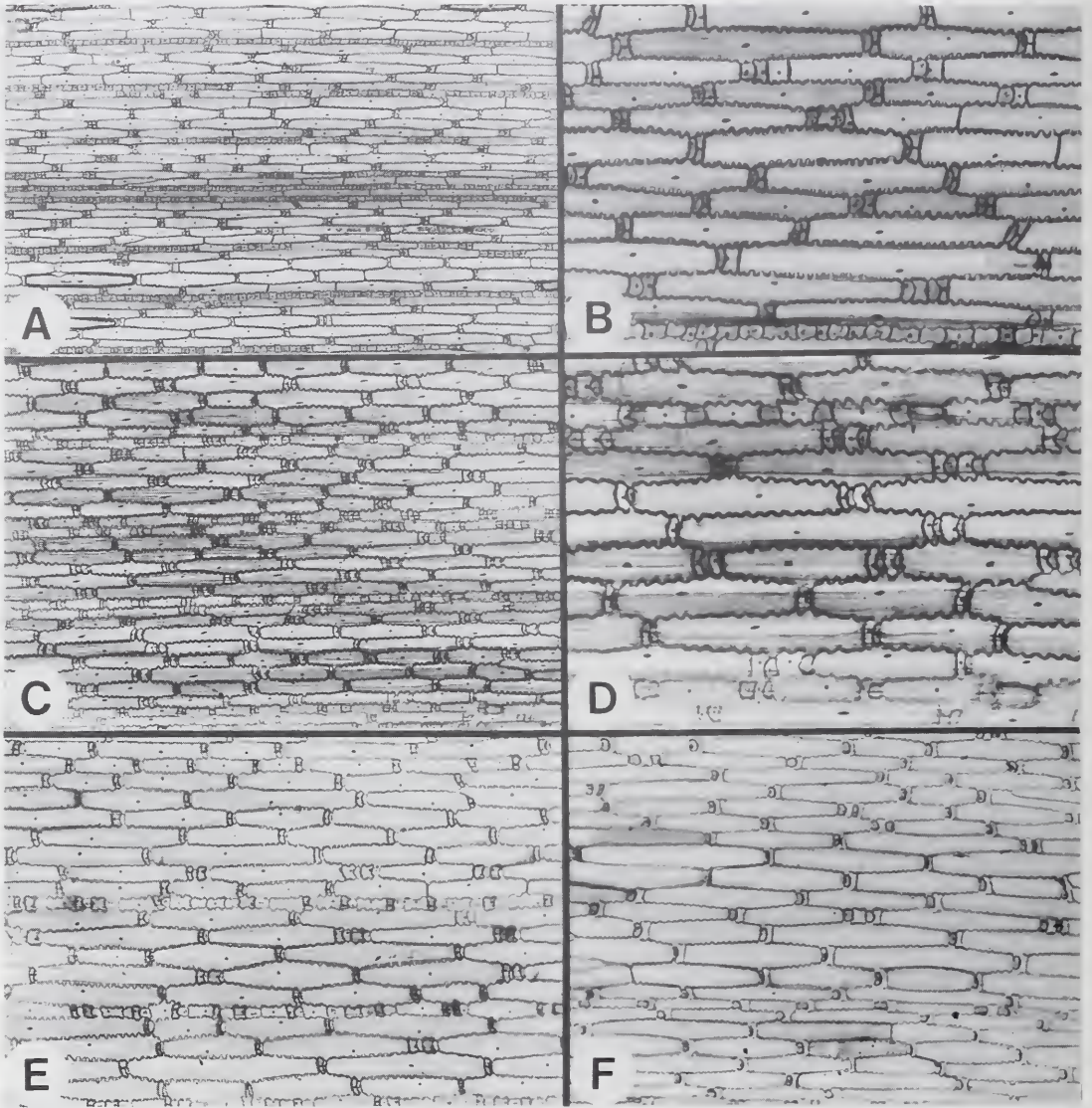


FIGURE 59.2.—*Pentaschistis acinosa*: abaxial epidermal structure.

A, epidermal pattern with slight zonation evident although the costal zones are very irregular.

B, detail of fusiform long cells with sinuous walls separated by pairs of tall and narrow short cells; note the very irregular dumbbell-shaped silica bodies associated with the costal zones.

C, specimen in which zonation is even less distinct than in A.

D, long cells alternating with groups of short cells; note the very irregularly shaped silica bodies located in the poorly defined costal zone.

E, fusiform long cells and very narrow costal zones with irregularly dumbbell-shaped silica bodies.

F, regular epidermal pattern with distinctly fusiform long cells.

A, B, *Ellis* 5560; C, D, *Ellis* 5550; E, *Ellis* 5549; F, *Ellis* 2340. A, C, $\times 160$; E, F, $\times 250$; B, D, $\times 400$.

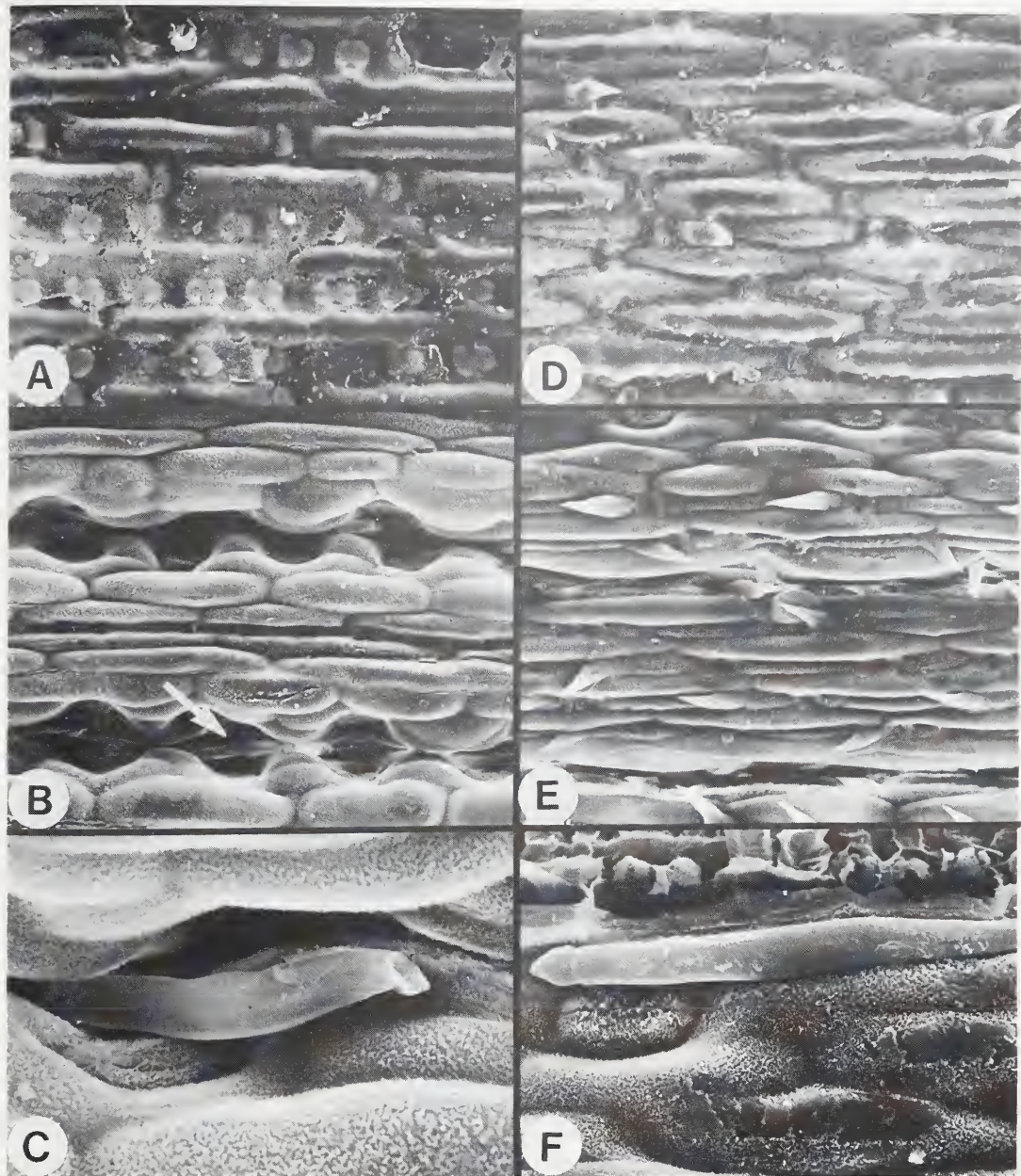


FIGURE 59.3.—*Pentaschistis acinosa*: leaf blade ultrastructure. A, D, abaxial epidermis. B, C, E, F, adaxial epidermis. A, rectangular long cells; note irregular dumbbell-shaped silica bodies. B, rather inflated adaxial epidermal cells, particularly those located on the sides of the cleft-like furrows; note microhairs in these furrows. C, microhair with very tiny adaxial cell. D, fusiform abaxial long cells with few very small hooks. E, adaxial surface with less inflated cells than in B; note small prickles. F, elongate, slender adaxial microhair with minute distal cell still intact. A, Ellis 5560; B, C, Ellis 5549; D–F, Ellis 4678. A, B, D, E, $\times 200$; F, $\times 480$; C, $\times 780$.

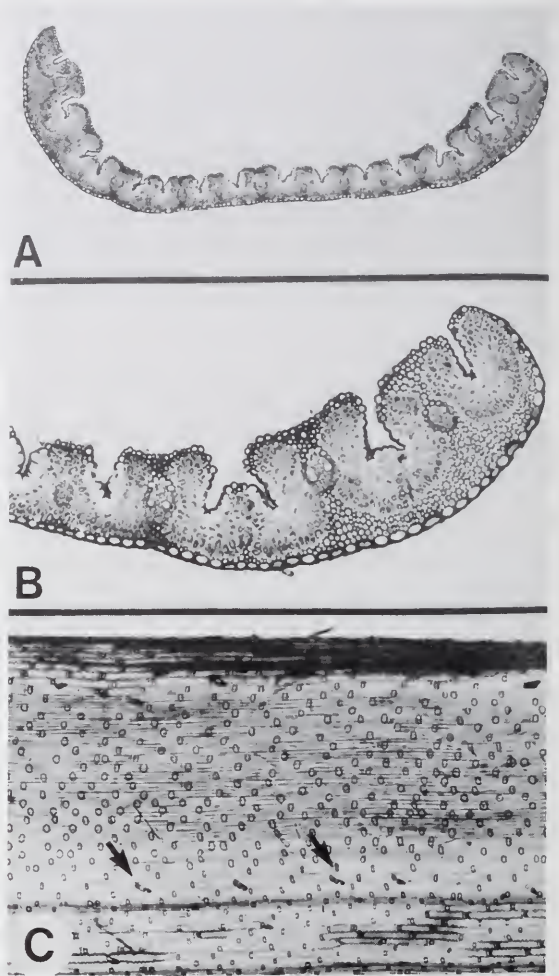


FIGURE 60.1.—*Pentaschistis caulescens*: leaf blade anatomy.

A, narrow but expanded leaf outline with thickened lateral parts structured in such a way that the margins interlock on infolding.

B, detail of leaf margin showing sclerenchyma distribution, adaxial ribs and furrows and abaxial microhair (arrowed).

C, abaxial epidermis showing greater width of cells overlying the thickened margin; note absence of stomata, rounded silica bodies and frequent microhairs (arrowed).

A–C, *Ellis 2482*. A, $\times 100$; C, $\times 160$; B, $\times 250$.

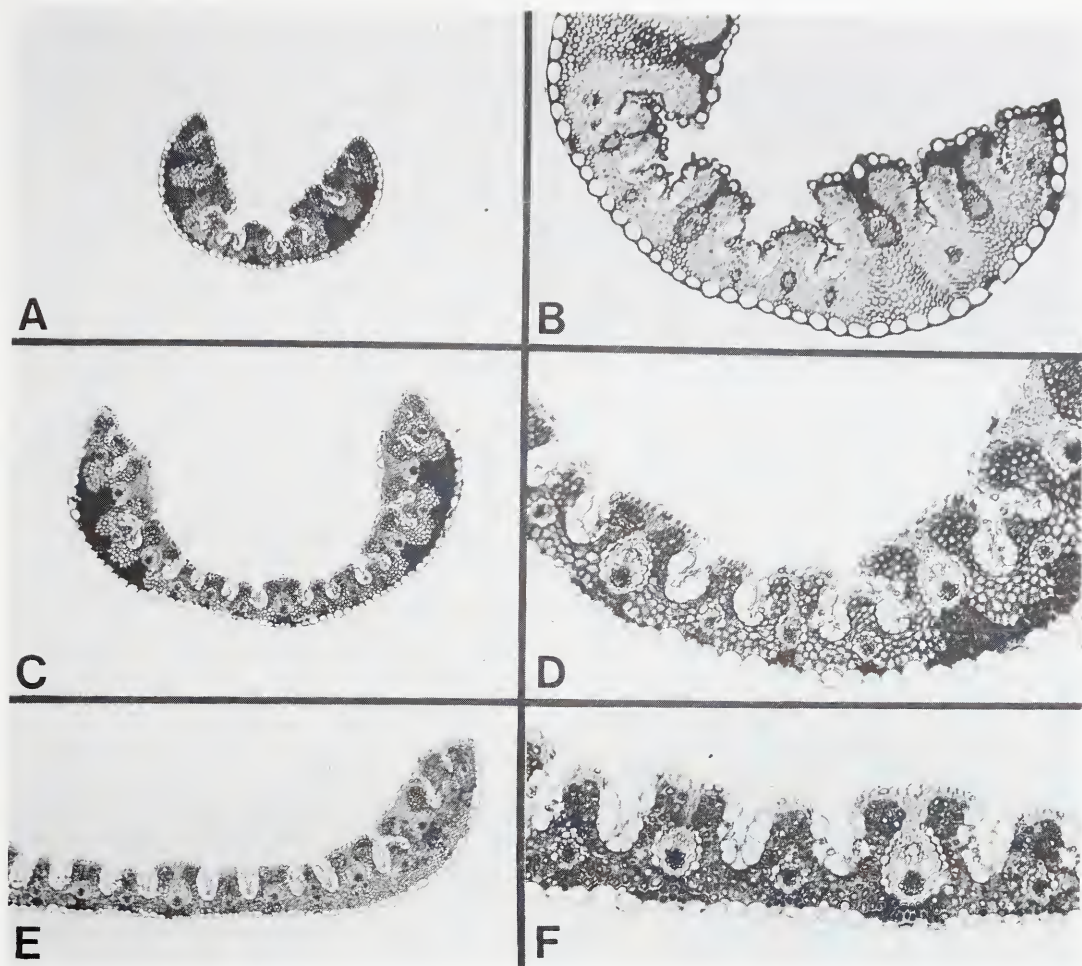


FIGURE 61.1.—*Pentaschistis scandens*: transectional leaf blade anatomy.

A, very narrow, setaceous leaf blade outline.

B, detail showing much thicker margins than midlamina; note consistently larger abaxial epidermal cells and bulliform cells on the sides and bases of adaxial furrows.

C, slightly wider blade also with prominently thickened margins; note copious abaxial sclerenchyma in margin.

D, alternating vascular bundle sequence and sclerophyllous type mesophyll.

E, expanded, open blade with thickened margin.

F, anatomical detail of compact chlorenchyma tissue and bulliform cells situated on the sides as well as the bases of the adaxial furrows.

A, B, *Ellis* 5988; C, D, *Ellis* 5987; E, F, *Ellis* 5986. A, C, E, $\times 100$; B, D, F, $\times 250$.

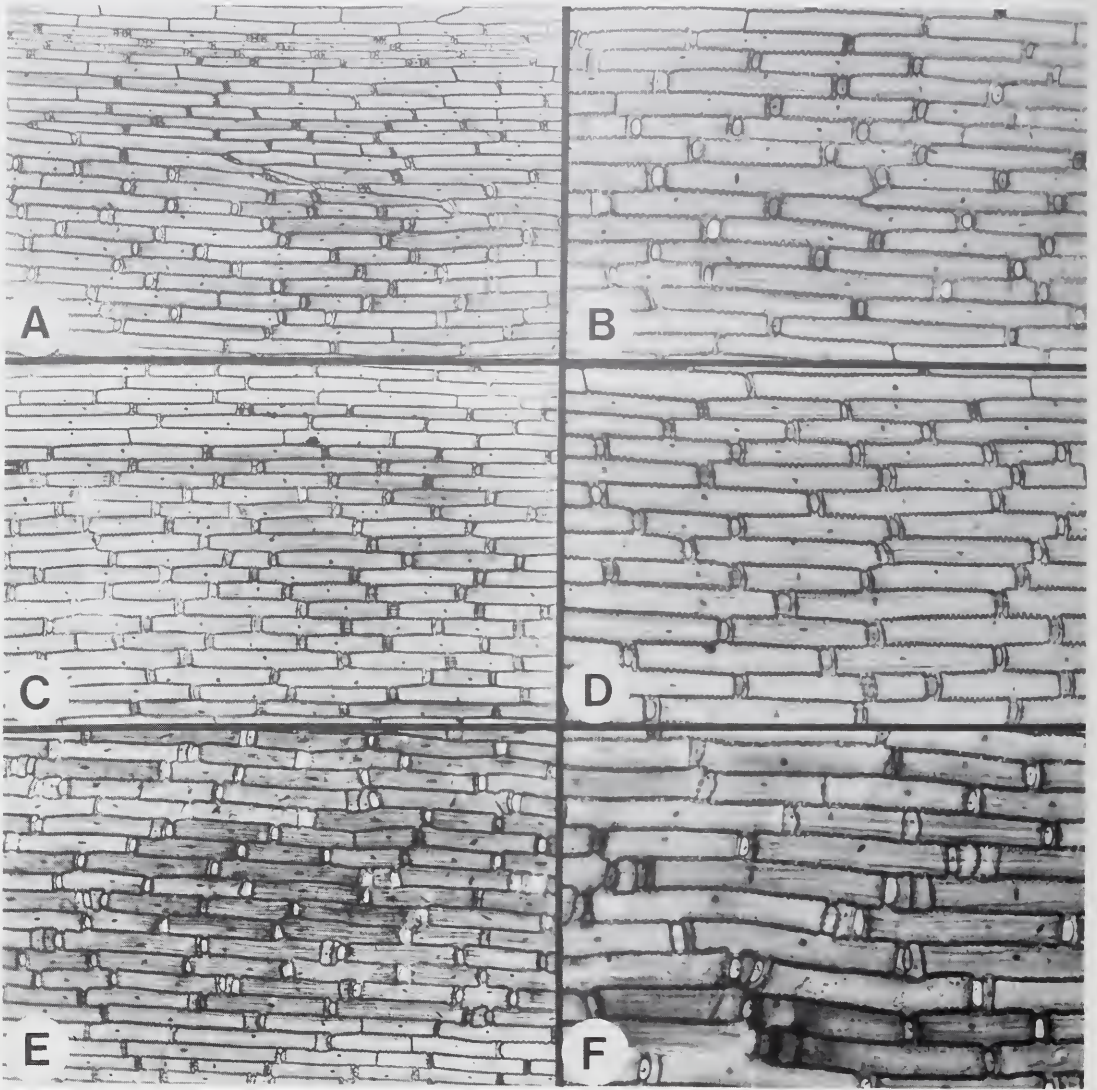


FIGURE 61.2.—*Pentaschistis scandens*: abaxial epidermis.

- A, epidermal zonation showing absence of zonation; note narrower cell files overlying the midlamina (at top of photograph) gradually increasing in width laterally.
 B, detail of rectangular long cells with thickened, sinuous walls; elliptical silica bodies closely associated with tall and narrow cork cells occur between all long cells.
 C, epidermal pattern with slight size difference between midlamina cell files (top) and those overlying the thickened margin (bottom).
 D, detail of long cells and alternating cork-silica cell pairs.
 E, uniform epidermal pattern with no zonation evident.
 F, detail of long cells and alternating short cells; short cells vary from pairs to groups of up to four cells.
 A, B, *Ellis* 5988; C, D, *Ellis* 5987; E, F, *Ellis* 5986. A, C, E, $\times 160$; B, D, F, $\times 250$.

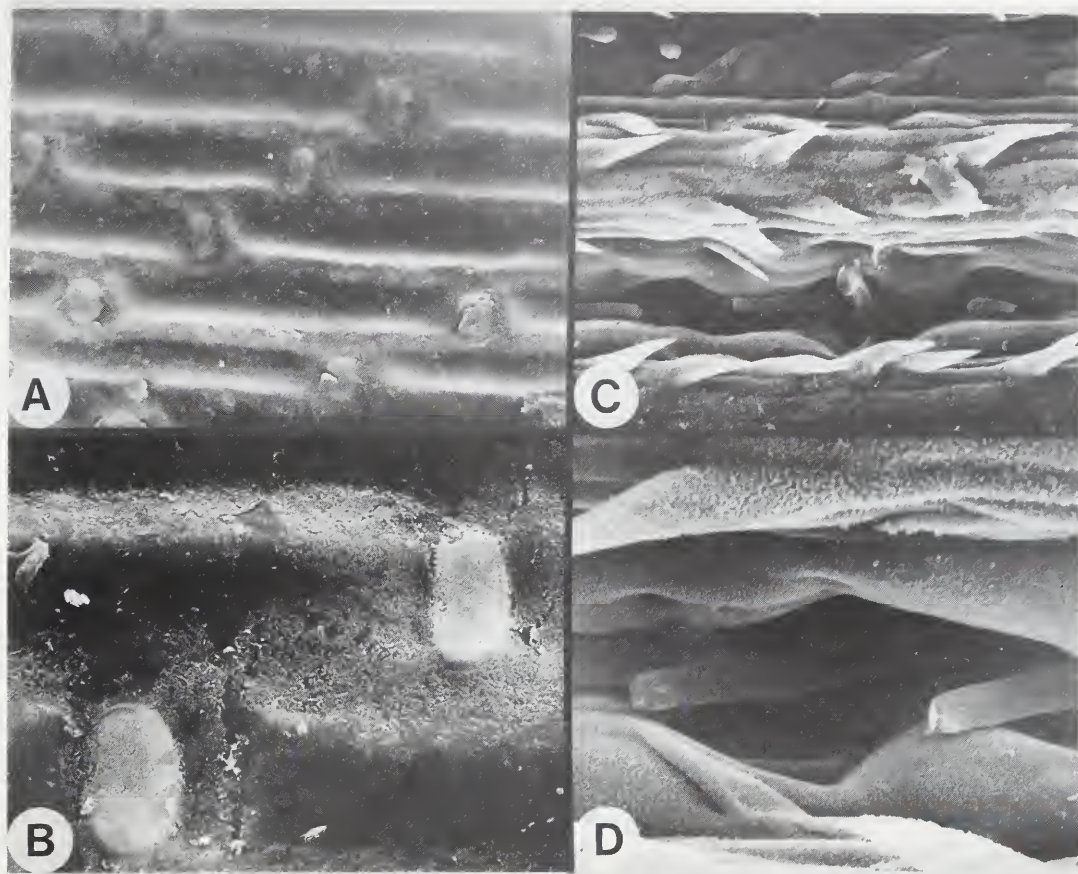


FIGURE 61.3.—*Pontaschistis scandens*: leaf blade ultrastructure. A, B, abaxial surface. C, D, adaxial surface. A, rectangular long cells with inflated periclinal walls and thickened anticlinal walls; note alternating silica bodies. B, detail of elliptical silica bodies. C, adaxial ribs and furrows; note prickles and microhairs located in the furrows. D, slender, finger-like microhairs in adaxial furrow; small distal cells not present. A, C, D, *Ellis* 5986; B, *Ellis* 5988. A, C, $\times 200$; D, $\times 560$; B, $\times 650$.

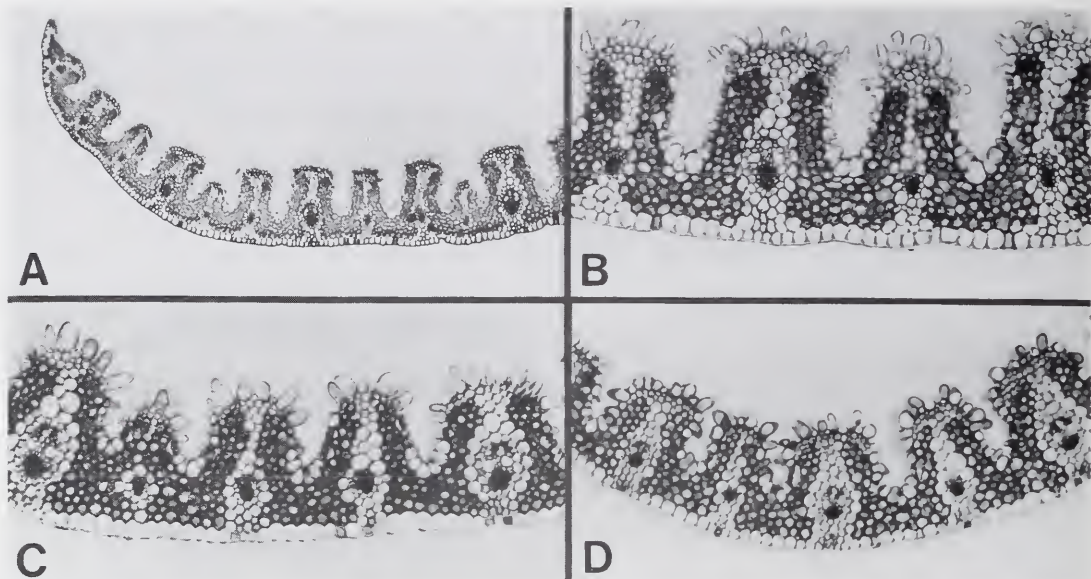


FIGURE 62.1.—*Pentaschistis capensis*: transectional leaf blade anatomy.

A, lateral part of lamina showing expanded nature of blade and tapering margin; note very irregular pattern of arrangement of vascular bundles with 2 or 3 variable smaller bundles between successive larger bundles.

B, detail of massive adaxial ribs and steep-sided furrows, bundle sheath extensions, compact type of mesophyll comprised of rather large, angular cells and abaxial epidermal cells larger than adaxial cells; note large, papillate cells scattered throughout adaxial surface.

C, globose, inflated papillae on adaxial surface, compact mesophyll and translucent outer bundle sheath and extension cells; the bundle sheath cells grade very gradually into collenchyma-like strands.

D, typical anatomy characterized by inflated adaxial papillae, compact mesophyll and conspicuous bundle sheath extensions.

A, B, *Ellis 5574*; C, *Ellis 5571*; D, *Linder 4600*. A, $\times 100$; B–D, $\times 250$.

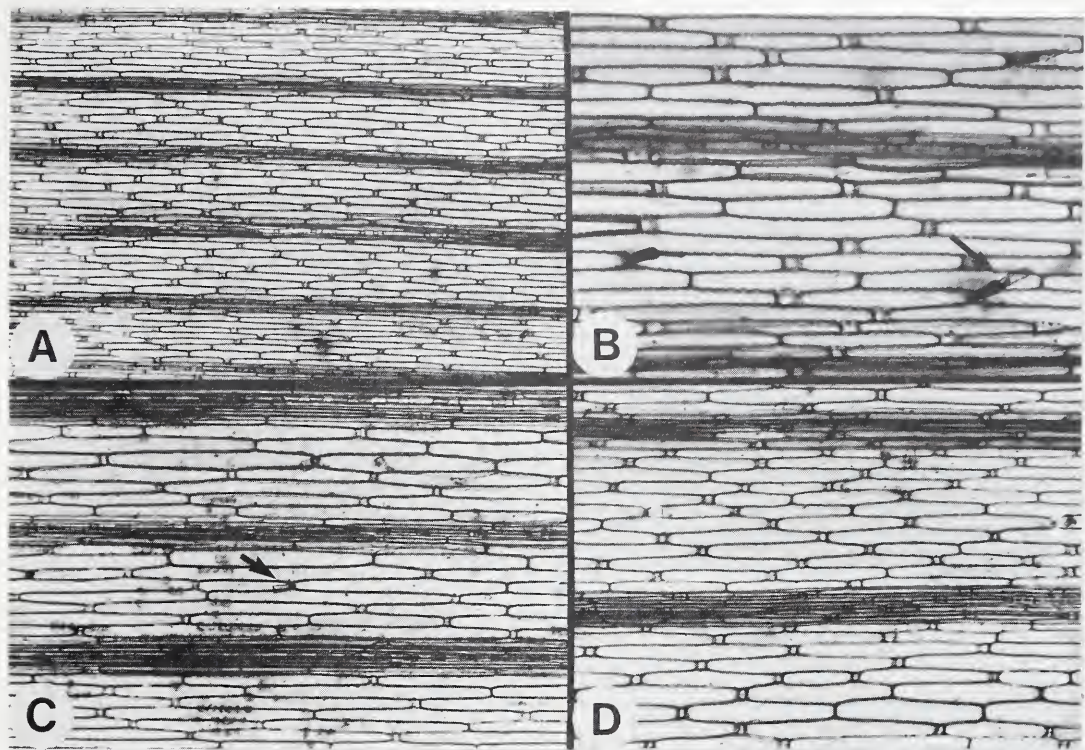


FIGURE 62.2.—*Pentaschistis capensis*: abaxial epidermal structure.

A, epidermal pattern showing clear zonation although differentiation of costal and intercostal cells only slight; costal zones distinguishable mainly due to staining of underlying collenchyma girders; no stomata present.

B, epidermal detail showing fusiform long cells alternating with single short cells; note microhairs (arrowed) with basal and distal cells about equal in length.

C, typical epidermal pattern; note dumbbell-shaped costal silica bodies and microhairs; stomata absent.

D, costal zones in which silica bodies are not strongly differentiated from those in the intercostal zones i.e. elliptical but tending to cross-shaped and very irregularly dumbbell-shaped.

A, B, *Ellis 557*; C, *Linder 4600*; D, *Ellis 5574*. A, $\times 160$; C, D, $\times 250$; B, $\times 400$.

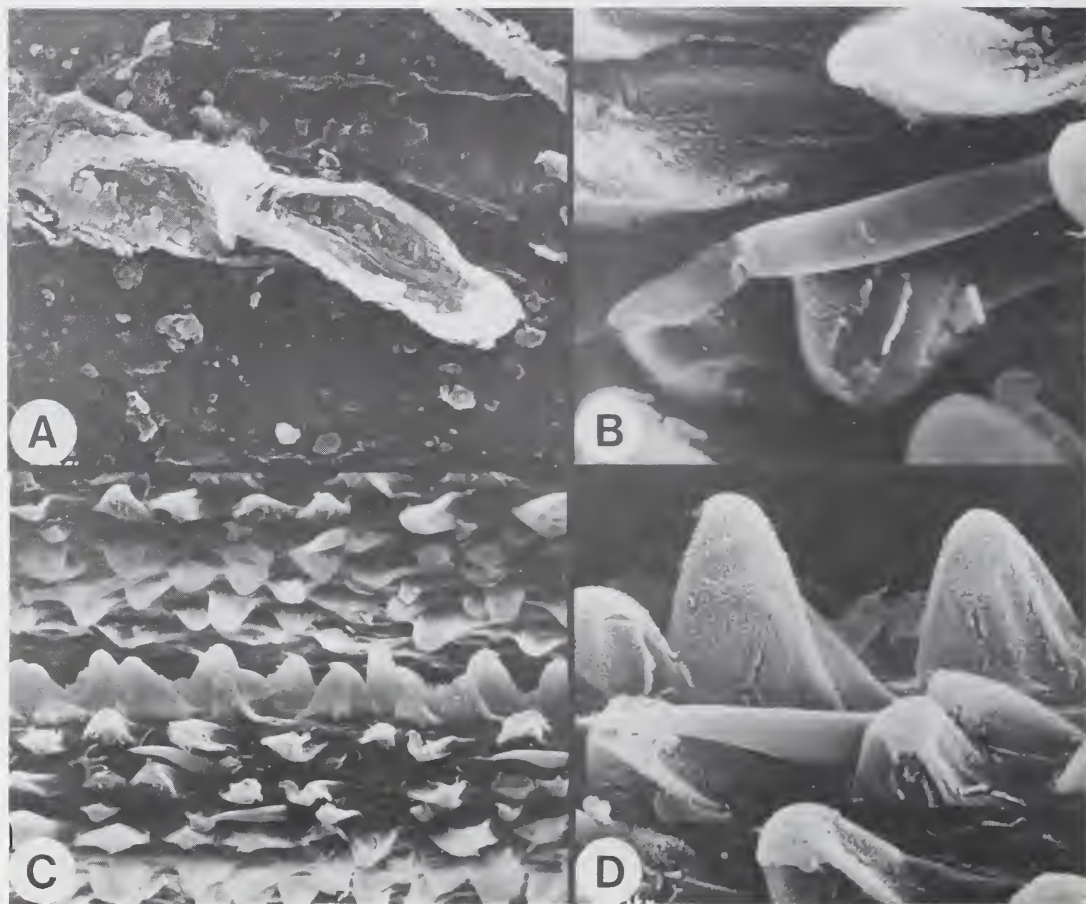


FIGURE 62.3.—*Pentaschistis capensis*: epidermal ultrastructure.

A, abaxial microhair with distal and basal cell approximately the same length.

B, adaxial microhair which is more slender and with a shorter distal cell than the adaxial hairs.

C, adaxial surface showing very elongate, inflated papillae on top of ribs and sides of furrows.

D, detail of globose adaxial papillae and prickly hair; note very fine epicuticular wax covering.

A–D, *Ellis 5571*. C, $\times 200$; D, $\times 650$; B, $\times 850$; A, $\times 1170$.

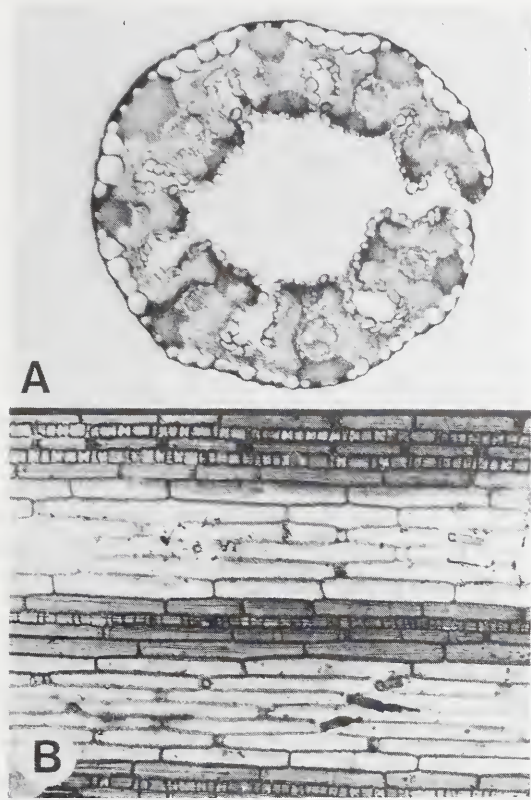


FIGURE 64.1.—*Pentaschistis andringitrensis*: leaf blade anatomy.

A, inrolled leaf blade outline with massive adaxial ribs and deep furrows; large trapezoidal abaxial, and inversely anchor-shaped, adaxial girders associated with all bundles and comprised of very thick-walled fibres; abaxial epidermal cells larger than inflated adaxial epidermal cells; chlorenchyma tissue poorly preserved but appears to be of the diffuse, mesic type.

B, abaxial epidermis with clearly differentiated costal and intercostal zones; no stomata, microhairs common and silica bodies irregularly dumbbell-shaped.

A, *Perrier 10832*; B, *Humbert 3919*. A, B, $\times 250$.



FIGURE 65.1.—*Pentaschistis humbertii*: transectional anatomy.

A, inrolled, but expanded leaf outline; prominent adaxial ribs and deep furrows with vertical sides; alternating first and third order vascular bundles; abaxial epidermal cells considerably larger than the smaller, but inflated, adaxial epidermal cells; mesophyll tissue poorly preserved but resembles the mesic type.

A, *Humbert 3310*. A, $\times 250$.

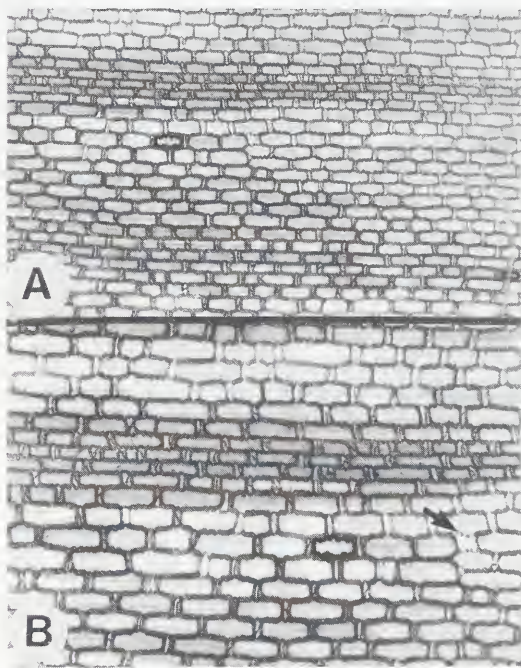


FIGURE 66.1.—*Pentaschistis chrysurus*: abaxial epidermal structure.

A, absence of epidermal zonation with uniform cellular pattern throughout.

B, detail of relatively short long cells alternating with cork-silica cell pairs in which both cells are tall and narrow; sometimes short chains of short cells occur (arrowed) and these resemble short sessile linear glands.

A, B, *Volgens 1826a*. A, $\times 160$; B, $\times 250$.

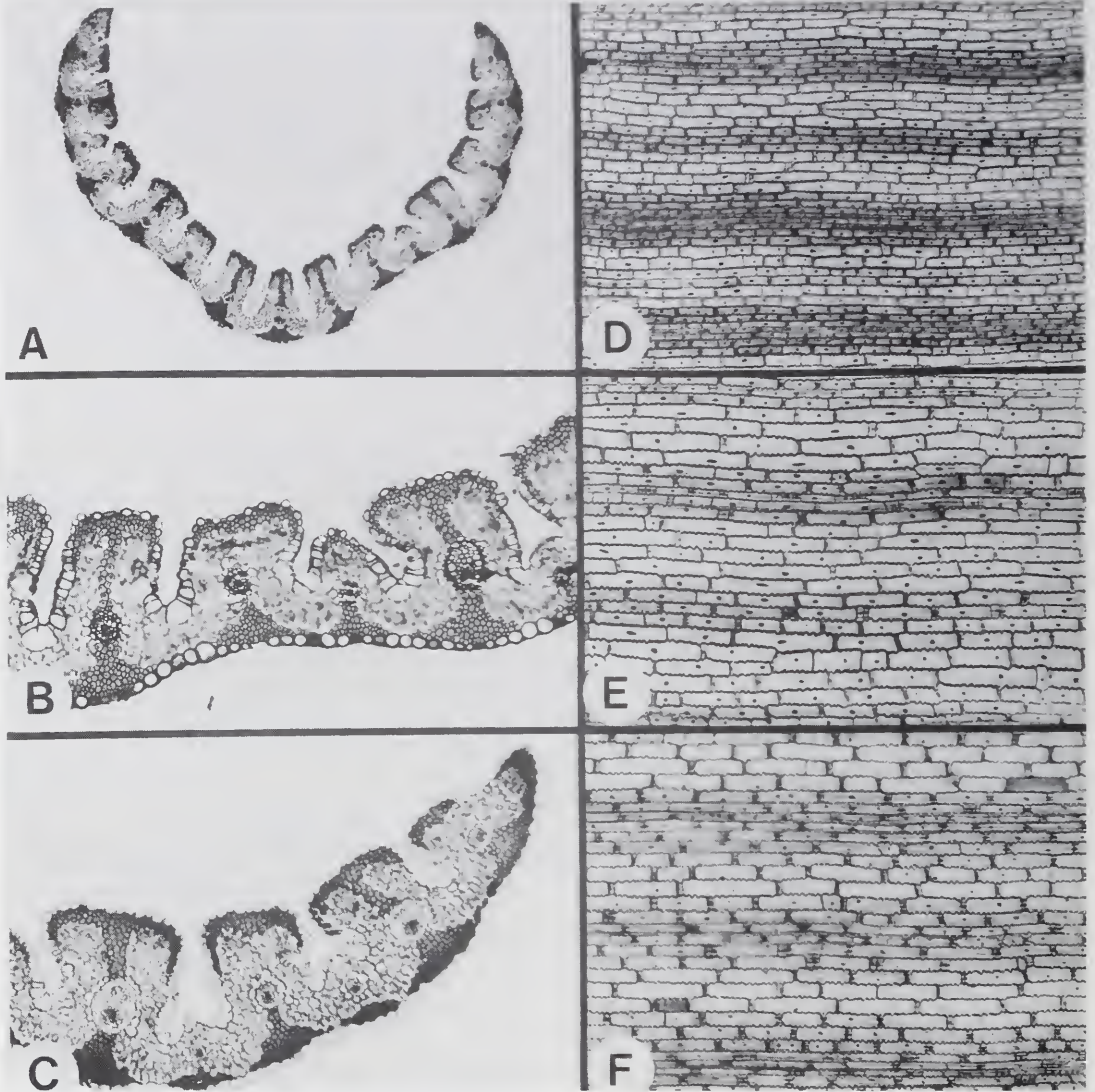


FIGURE 67.1.—*Pentaschistis heptamera*: leaf blade anatomy. A–C, transectional anatomy. D–F, abaxial epidermis. A, expanded but slightly infolded leaf blade. B, detail of variable, but well-developed adaxial ribs and cleft-like furrows; 2 or 3 smaller bundles interspaced between the first order bundles; adaxial sclerenchyma girders inversely anchor-shaped and the abaxial girders are broadly trapezoidal, tending to fuse laterally to form a continuous hypodermal layer. C, detail of margin showing ribs and girders and chlorenchyma structure; the chlorenchyma cells rather compact and angular but air spaces are visible. D, abaxial epidermal pattern with zonation poorly differentiated; costal zones not structurally different from the intercostal zones but distinguishable due to staining of underlying fibrous tissue; no stomata. E, detail of rectangular long cells with sinuous walls; central file of costal zone with narrower cells; all long cells nucleate. F, typical epidermis with both long and short cells nucleate; no silica bodies, stomata or microhairs visible. A, B, D, E, *Ellis 6007*; C, F, *Ellis 6008*. A, $\times 100$; D, $\times 160$; B, C, E, F, $\times 250$.

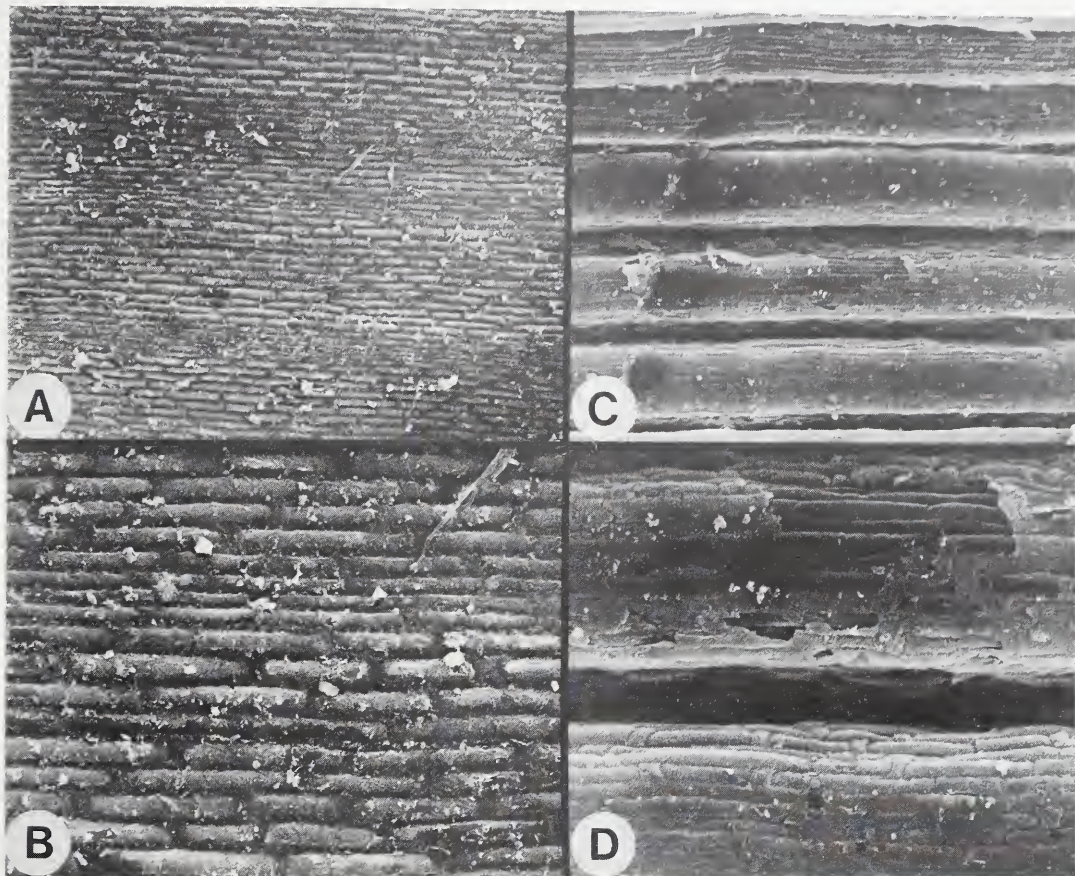


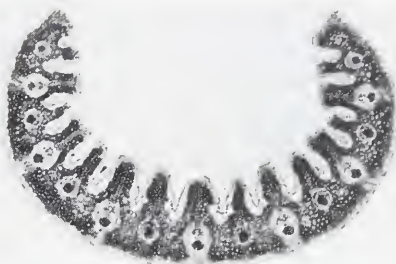
FIGURE 67.2.—*Pentaschistis heptamera*: epidermal ultrastructure. A, B, abaxial epidermis. C, D, adaxial epidermis. A, very uniform but featureless adaxial surface with no stomata or appendages. B, detail of brickwork pattern of long cell arrangement; long cells rectangular with slightly inflated periclinal walls. C, adaxial surface showing adaxial ribs and cleft-like furrows; no prickles or other appendages. D, detail of adaxial rib showing thick layer of epicuticular wax; no microhairs detected. A–D, *Ellis 6008*. A, C, $\times 60$; B, D, $\times 200$.

FIGURE 68.1.—*Pentaschistis eriostoma*: variation in transectional leaf blade anatomy.

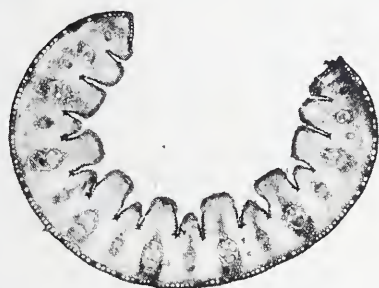
- A, tightly infolded, setaceous outline; note relative thickness of median part of lamina and lateral parts.
B, more open but nevertheless inrolled blade without lateral thickening.
C, narrow, inrolled blade with slight lateral thickening.
D, wider inrolled leaf with continuous hypodermal sclerenchyma visible; note asymmetrical margins.
E, very sclerified xeric leaf blade; note continuous abaxial sclerenchyma layer and symmetrical margins.
F, inrolled, cylindrical blade with asymmetrical margins; margins shaped so that when they come into contact a hollow cylinder will be formed.
G, interference contrast with refractive lignified sclerenchyma girders and hypodermal layer; note air spaces in the mesophyll but the abaxially located chlorenchyma cells are compactly arranged.
H, anatomical detail showing air spaces associated with mesophyll tissue located at the bases of the adaxial furrows; note prickles in adaxial epidermis.
A, *Ellis* 5513; B, *Ellis* 2444; C, *Ellis* 2486; D, *Ellis* 2581; E, *Ellis* 2502; F, *Ellis* 2584; G, *Ellis* 2491; H, *Ellis* 2473.
A–F, $\times 100$; G, H, $\times 250$.



A



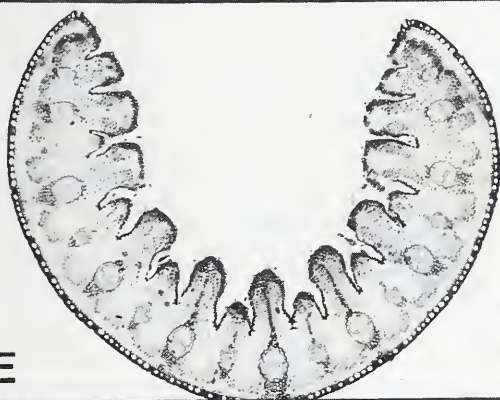
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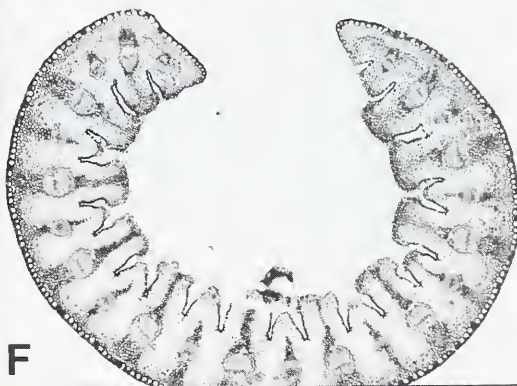
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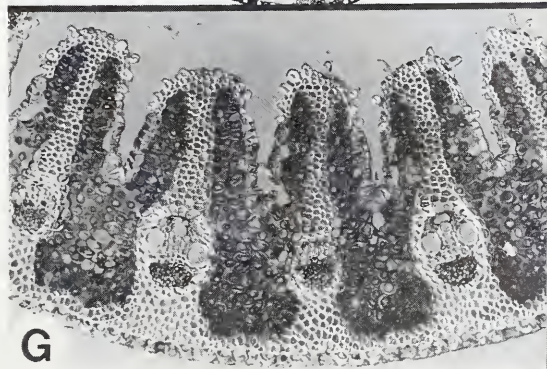
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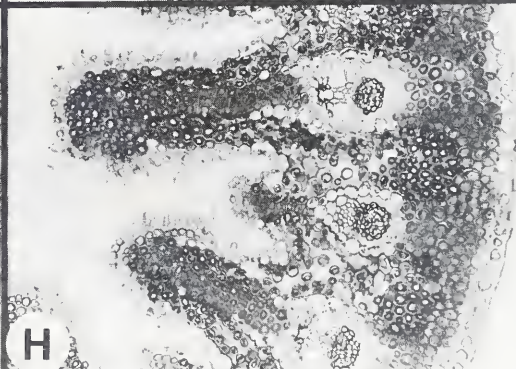
E



F



G



H

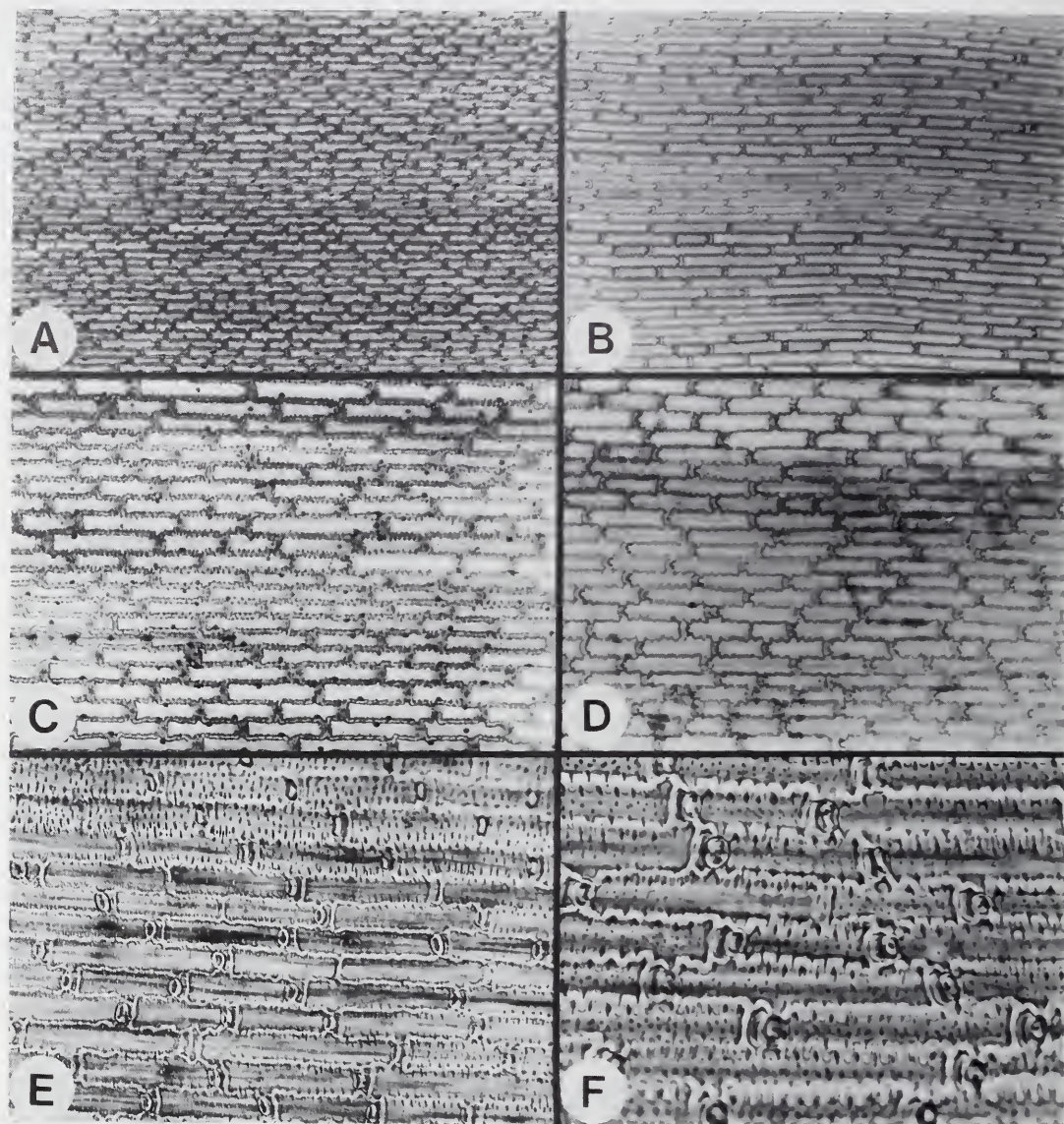


FIGURE 68.2.—*Pentaschistis eriostoma*: abaxial epidermis.

A, epidermal zonation not developed and entire epidermis of uniform long cells arranged in a brickwork pattern. B, undifferentiated epidermis although cells overlying abaxial sclerenchyma girders, or the costal zones, can be distinguished due to the underlying fibres.

C, long cells alternating with short cell pairs, the silica bodies being elliptical to rounded and narrower than the long cells; note very thick anticlinal walls and pitted periclinal walls.

D, pitted long cells and cork-silica cell pairs clearly evident; no appendages or stomata present.

E, detail of pits and elliptical silica bodies at varying focal planes.

F, sinuous, very thick, anticlinal walls and rounded silica bodies enfolded in crescentic cork cells.

A, *Ellis* 5627; B, *Ellis* 1177; C, *Ellis* 5128; D, *Ellis* 1297; E, *Ellis* 2473; F, *Ellis* 2502. A, B, $\times 160$; C, D, $\times 250$; E, $\times 400$; F, $\times 640$.

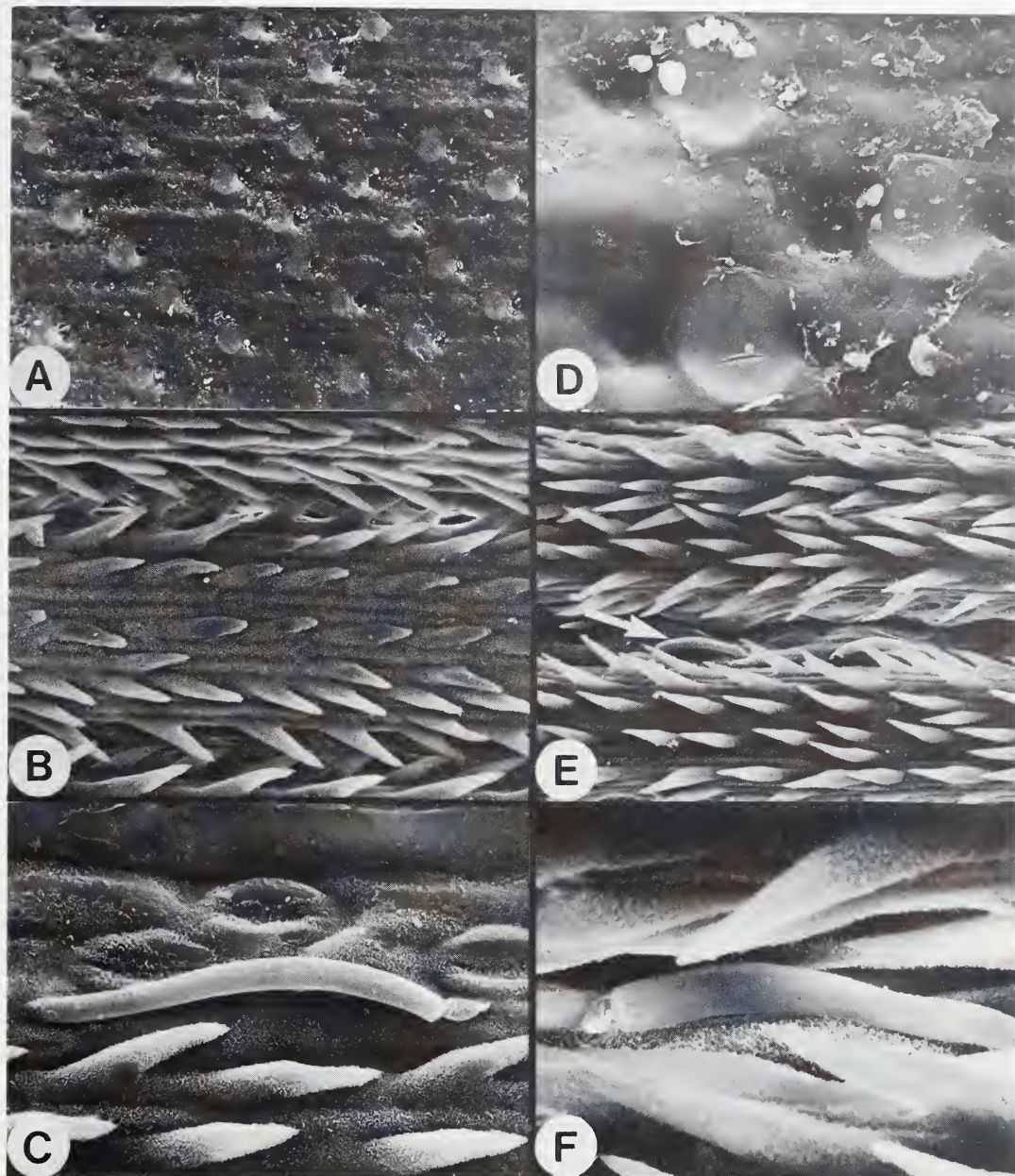


FIGURE 68.3.—*Pentaschistis eriostoma*: epidermal ultrastructure. A, D, abaxial epidermis. B, C, E, F, adaxial epidermis.

A, only silica bodies visible on abaxial surface; no appendages present.

B, adaxial rib with numerous prickles, these hairs slightly shorter on the apex of the rib than on the sides where they interlock over the deep, cleft-like furrows.

C, elongate, very narrow adaxial microhair with minute distal cell; note stomata with slightly raised subsidiary cells.

D, detail of circular abaxial silica bodies.

E, typical adaxial surface with prickles; note microhair located in adaxial furrow (arrowed).

F, detail of slender microhair with minute distal cell located amongst adaxial prickles.

A–C, *Ellis 5128*; D–F, *Davidse 33577*. A, B, E, $\times 200$; C, $\times 500$; F, $\times 800$; D, $\times 1050$.

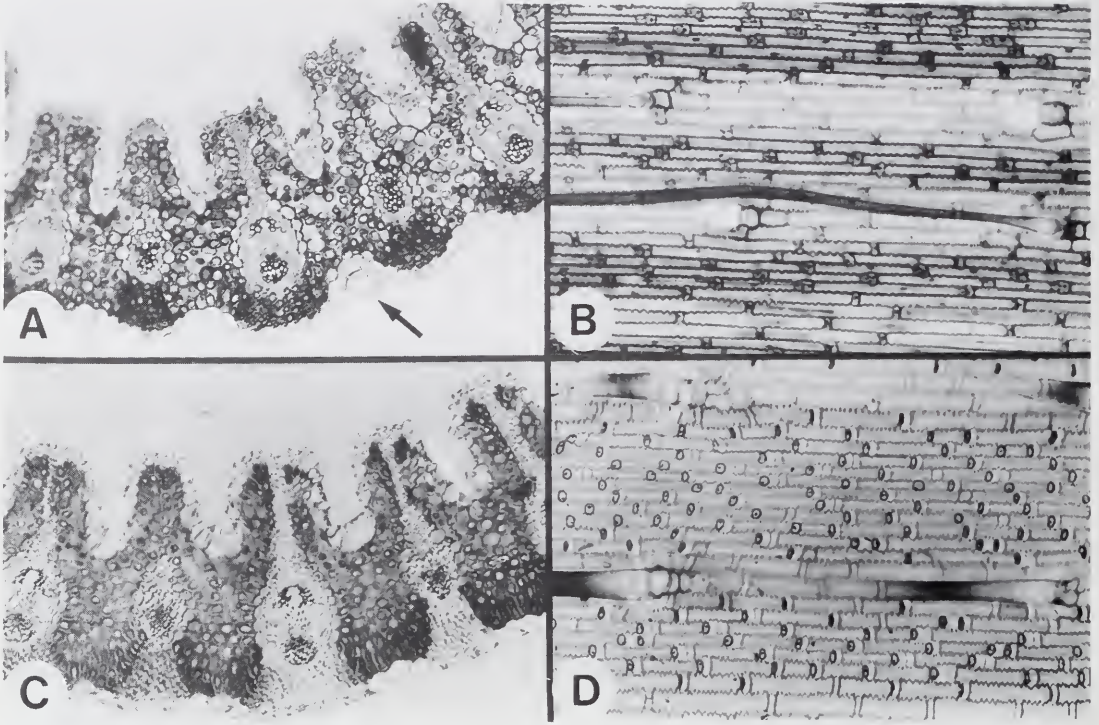


FIGURE 68.4.—*Pentaschistis eriostoma*: specimens with atypical leaf blade anatomy.

- A, transverse section showing abaxial ribs and furrows; note sectioned macrohair located at the base of an abaxial furrow (arrowed).
 B, abaxial epidermis showing very elongate macrohairs with slightly swollen bases lying along the abaxial intercostal zones.
 C, specimen with adaxial macrohairs inserted in the bulliform cells at the bases of the furrows; note that a continuous abaxial hypodermal layer is not present.
 D, abaxial macrohair structure; note swelling towards base and superficial insertion between a few modified epidermal cells.
 A, *Ellis 5152*; B, *Ellis 5455*; C, D, *Ellis 667*. A–D, $\times 250$.

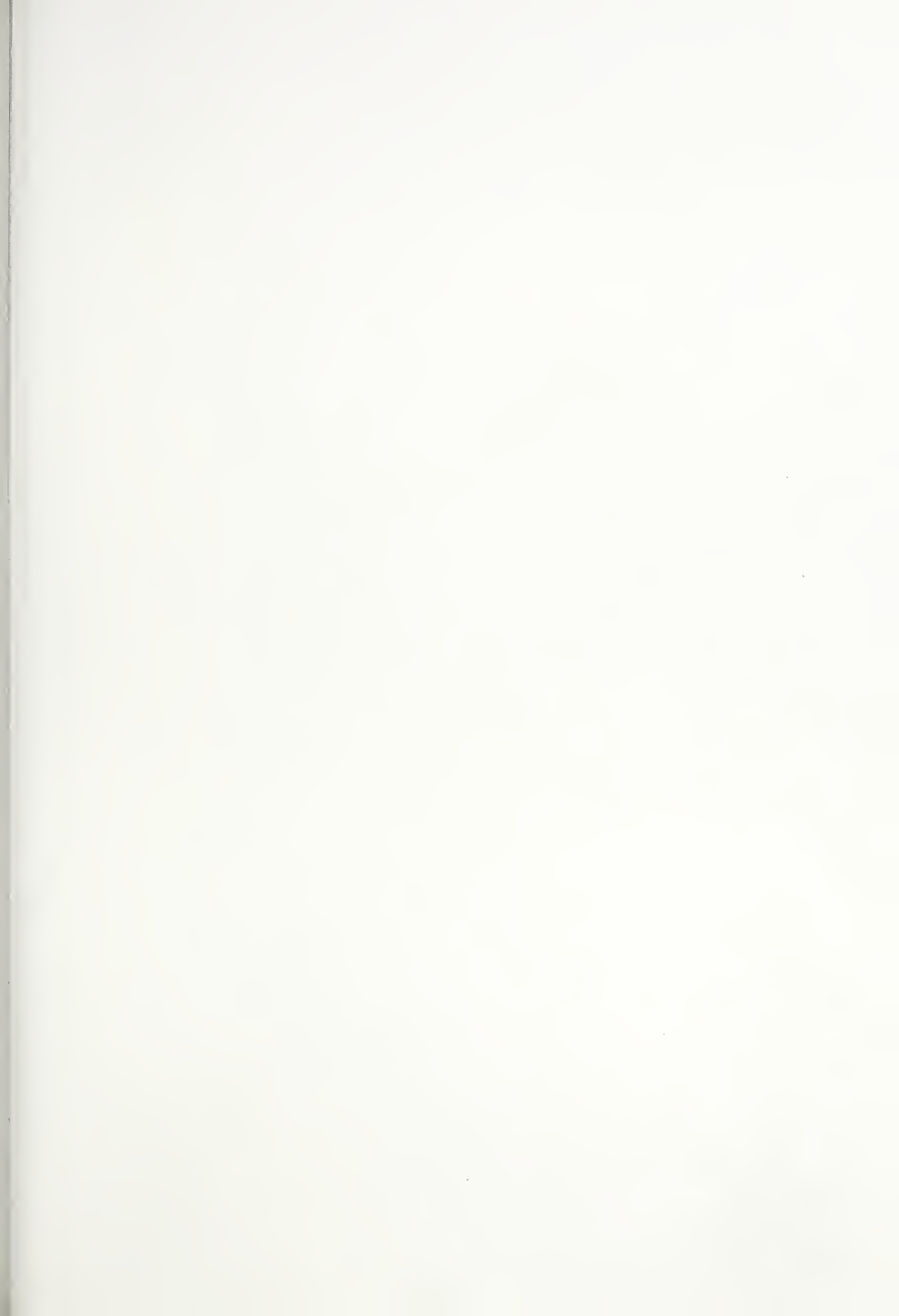
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